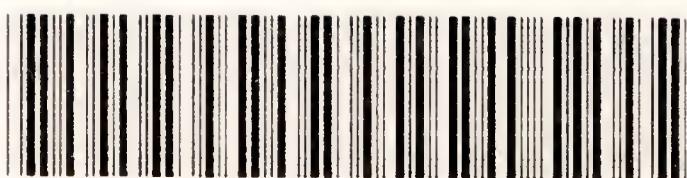




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THREE LECTURES
ON NEUROBIOTAXIS AND OTHER SUBJECTS,
DELIVERED AT THE UNIVERSITY
OF COPENHAGEN

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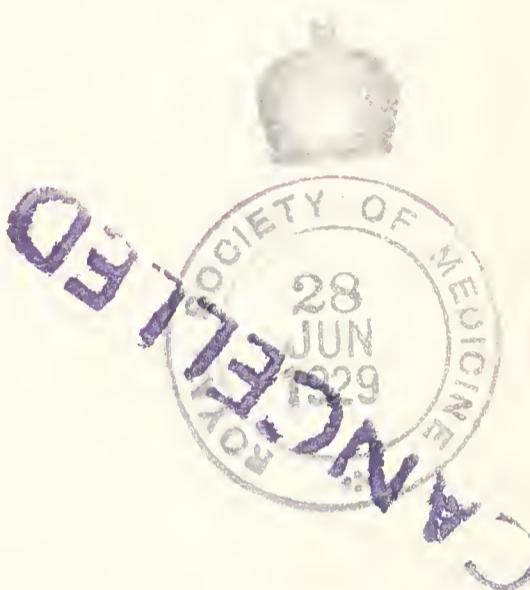
THREE LECTURES

ON NEUROBIOTAXIS AND OTHER SUBJECTS,

DELIVERED AT THE UNIVERSITY OF COPENHAGEN,

BY

C. U. ARIËNS KAPPERS,
AMSTERDAM.



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PREFACE.

These lectures, delivered at the University of Copenhagen under the auspices of the Rask-Ørsted fund, and later at the Universities of Lund and Upsala, and in Svenska Läkerasellskapet, Stockholm, are reprinted from the *Acta Psychiatrica et Neuropologica*, managing editor Dr. K. H. Krabbe.

By the courtesy of the editor and the publishers, to whom I am greatly indebted, they are now issued in this form.

I take this opportunity to express my gratitude for the hospitality received from my Scandinavian colleagues in the spring of 1927.

C. U. Ariëns Kappens.



ON NEUROBIOTAXIS, A PSYCHICAL LAW IN THE STRUCTURE OF THE NERVOUS SYSTEM.

In the first of these lectures I should like to speak about a causal relation in the structure of the brain, the knowledge of which is based chiefly on comparative anatomical researches.

The structural relation referred to is the material analogy to a mental relation long known in psychology, the law of association, already mentioned by *Aristotle*.

We all know, that if we have often heard a certain tune in the presence of a certain person, the mental images of this person and of this tune will become connected, associated, in our mind.

These associations are greatly used in instruction. Thus, for instance, when teaching children the pronunciation of the letters of the alphabet we utter certain sounds and at the same time show them certain letters, and on account of their simultaneity the impression of the sound and the visual impression remain connected in the children's memory.

This process of association is by no means the sole factor in the structure of our spiritual life, but it is a very important one.

Do we find indications in the anatomy of the brain that this mental law may also be observed in the structure of the nervous system?

In the following pages I shall discuss some structures which

seem to give us an answer to this question. — I will start with a simple example.

The skin of the head receives its sensory nerves from several roots, especially the V and the upper cervical nerve, in fishes the 1st, in man the 2nd dorsal cervical root chiefly.¹⁾

As the extensions of these nerves on the head border directly upon and even partly overlap each other, it is evident that these nerves are often stimulated at the same time.

Now we see that centrally the fibres of these nerves meet because the trigeminus, after its entrance into the oblongata, runs a long way downwards, descending to the sensory region of the 1st (or 2nd) cervical nerve, so that the offshoots of both nerves have a common centre of termination in the upper cervical cord (fig. 1). —

This junction of nerve fibres is evidently based upon the fact that these fibres are often stimulated at the same time: their function thus being simultaneously associated.

That this simultaneous function is really the cause of this anatomical correlation is clearly illustrated by the following fact.

Besides the above named nerves, still another nerve takes part in the cutaneous innervation of the head, although for a small part only.

This nerve, the N. vagus, however, chiefly contains fibres which do not proceed to the skin, but to the gullet and the intestines.

Now it is evident that the latter fibres of the vagus are never stimulated at the same time as the skin of the head. —

Stimulations simultaneous with those of other nerves of the head occur only with those branches of the vagus which also pass to the head (in man to the ear and the external auditory canal).

Now as the N. vagus enters the oblongata we see that its fibres immediately divide into two groups, the greater of which

¹⁾ The dorsal root of the 1st cervical nerve in man is very small.

(largely gustatory fibres in the cod) terminates in a medio-dorsal part of the oblongata, while the other group — that of the above-named skin fibres — joins the skin fibres of the trigeminus (fig. 1) and descends with it.

Consequently we also here find a connection of cutaneous fibres of the head with other cutaneous fibres of the head,

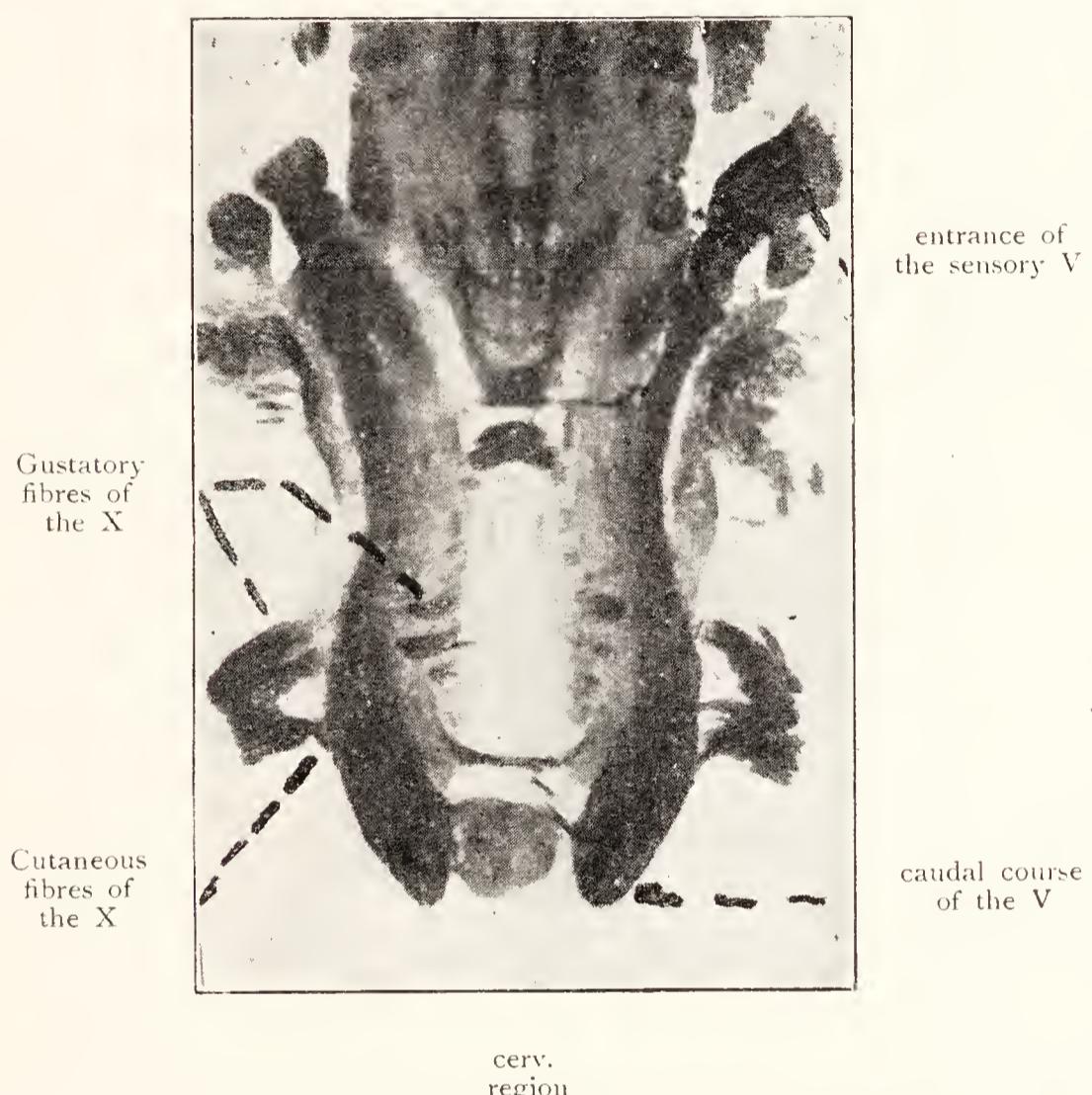


Fig. 1.

Horizontal section of the oblongata of a codfish, showing the course of the descending V root to the cervical region and the cutaneous fibres of the X joining this root.

evidently based upon their associated function, so that this is a material connection based upon simultaneous stimulation.

A similar process is observed in the fibers carrying the sense of taste. The sense of taste, in man principally localized on the

tongue and palate, is innervated here by two nerves, the VII and the IX, which enter the central nervous system at places, that are wide apart.

The peripheral branches, however, of these nerves lie close together upon the tongue, even partly overlap, and are practically always stimulated at the same time. —

The consequence of this is that the central axons of these nerves join in the oblongata, ending in a centre, in which in fishes also taste fibres of the vagus end.

Therefore the fibres of the VIIth root descend a considerable distance in order to reach the centre of the IXth (and Xth) nerve (fig. 2).

Thus also here we find a junction between the offshoots of two different roots as a consequence of simultaneous stimulation (simultaneous function).

This process is seen in still another form in connection with taste. It is well known that the organs of taste and smell are often stimulated simultaneously. Thus if we drink a fragrant drink, we taste and smell that drink simultaneously.

As a result of this, an anatomical correlation between the centres of smell and taste is established, a connection that is the more striking as smell is innervated by the 1st. nerve and taste by the VIIth, IXth (and Xth) and their centres consequently lie at a great distance from each other in the brain.

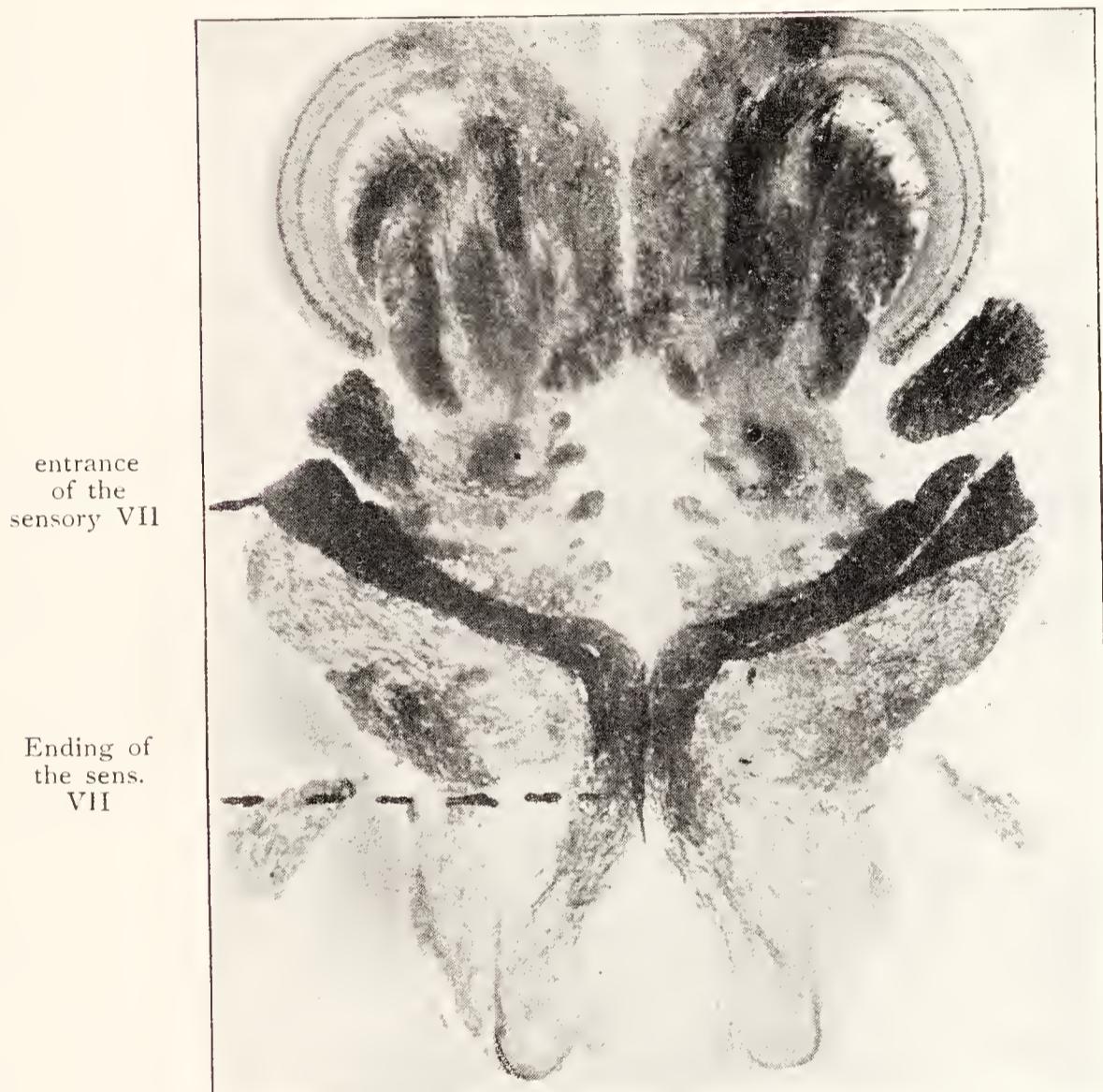
The tertiary connection, however, between these two centres, is very distinct in some fishes (where taste and smell are more developed than in man) and is caused by a bundle, which, originating in a secondary taste centre of the oblongata, passes through the midbrain ending in a region of the hypothalamus (*Herrick*), where also tertiary olfactory tracts from the forebrain end.

These are simple examples of the neurotropic influence of simultaneous and successive stimulations which I have called *neurobiotactic processes*, because they are processes of taxis or tropism, occurring during life in the nervous system.

It is not surprising that the motor centres in the nervous system are also strongly influenced by these processes.

In fact, the motor nuclei were the first centres, in which I observed this phenomenon (1907). The consequences are more striking here than in the sensory regions, important topographic differences of homologous cellgroups being called forth. The following pictures illustrate some examples.

Figures 3—6 are taken from animals, living under dif-



sens. IX and X nucl.

Fig. 2.

Horizontal section of the oblongata (and midbrain) of the cod-fish, at a level dorsal to fig. 1. Caudal course of the sensory VII roots to the sens. IX and sens. X nucleus.

ferent conditions, some in water, others on land, and of which the bulbar nuclei are influenced differently by the different ways which the animals are organized and live.

Fig. 3 left hand, at the top shows the sensory centre of the gills (nucl. gust) of a shark.¹⁾

This centre influences a motor nucleus that innervates the VII muscles.

The sensory centre itself is stimulated by impulses from the water in which the animal lives and by the condition of the

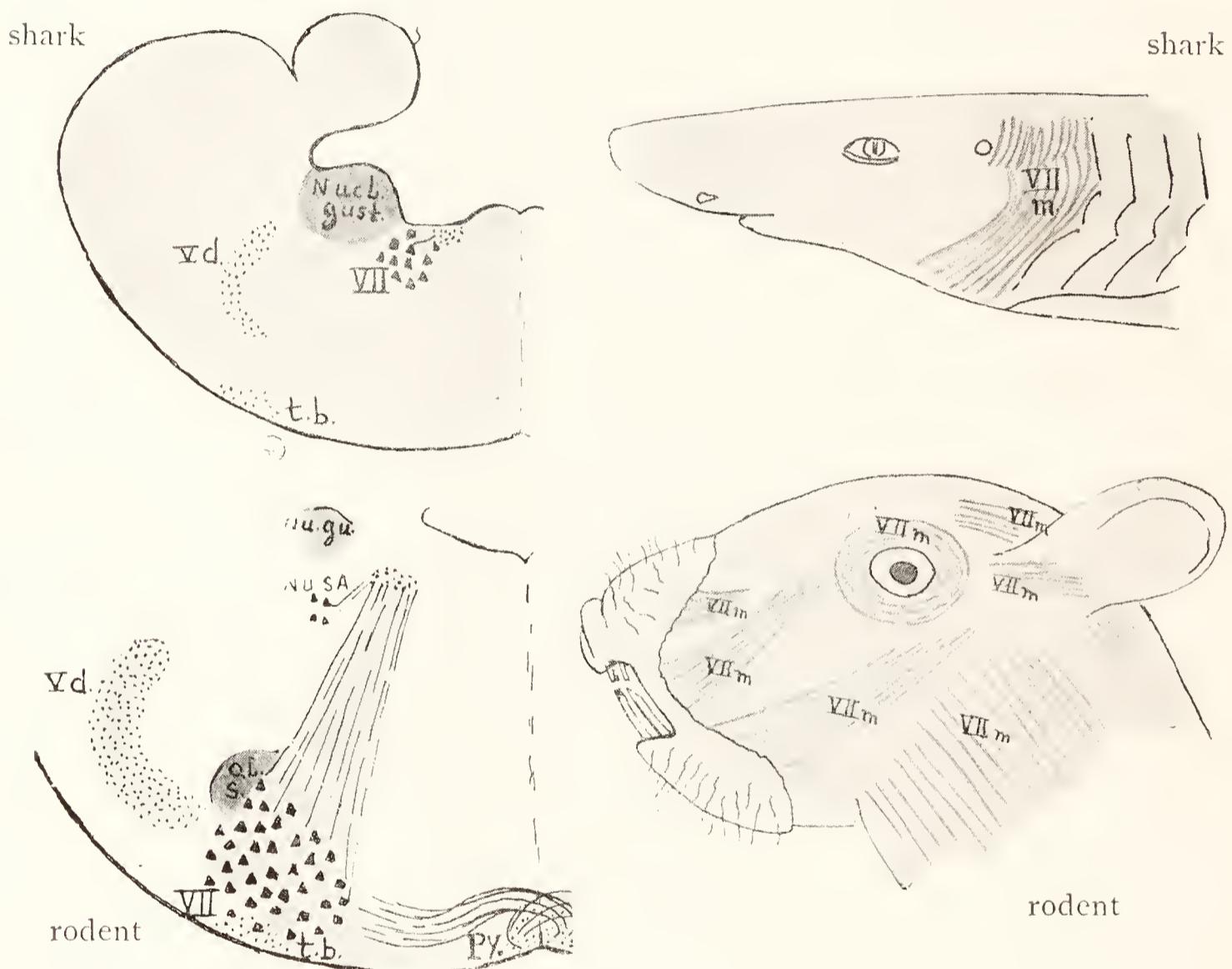


Fig. 3.

Above: sensory and motor VII centers in a shark (left side) and (right side) extension of the superficial VII musculature in the gill region of this animal.

Below: the different (mostly) ventral reflex centres of the (ventral) motor VII nucleus in a rodent and extension of the VII musculature in this animal.

¹⁾ This is called nucl. gustatorius because the taste fibres also terminate here next to general viscero-sensory fibres.

gills, which are at different times more or less saturated with oxygen or with the metabolic products of respiration.

As these impulses are transmitted by short neurones to the motor VII nucleus the motor centre of the VII lies very near this sensory nucleus, at the dorsal side of the brainstem.

If we compare with the above the topography of the homologous centre of a rodent (fig. 3, below), we find a very different location of the motor VII nucleus.

To explain this we must realize that animals, when adapting themselves to life on land, lose their gills. The muscles originally used for gill- or associated movements acquire another function. In mammals they grow over the face and establish connections with the mouth, nose, ears, and eyes.¹⁾ It is quite evident that the stimulations which now influence the motor VII nucleus are very different from those in fishes.

Whereas in sharks impulses from the mucous membranes of the gills (among them taste) dominate the motor VII nucleus, in mammals many cutaneous impulses from the surroundings of the mouth, nose, eyes and ears in addition to optic and acoustic impulses influence this centre.

Whereas the proprioceptive impulses of the facial muscles keep their course in the facial root (*Davis*,²⁾ *Gerard*³⁾ the above mentioned impulses do not enter by the sensory VII root (which is very much reduced in mammals) but enter the facial nucleus by means of the trigeminus and other reflex paths localized near the base of the oblongata.

Thus the sensory fibres of the mouth, nose and eyes run in the trigeminus (V d.), a secondary centre of the cochlea, causing reflexes of the ear-muscles, lies at the base (oliva superior: Ol.S.,

¹⁾ For the development of the facial muscles in vertebrates, especially in mammals I refer to the papers by *Ernst Huber* in the *Anatomische Anzeiger*, Bnd. 51, 58, 59, 61, 61 and the *Journ. of Comp. Neur.* Col. 42, 1927.

²⁾ *Davis*. The deep sensibility of the face. *Am. Archives of Neurology and Psychiatry* Vol. 9, 1923.

³⁾ *Gerard*. Afferent impulses of the trigeminal nerve. *Ibidem*. The results of these authors were confirmed by an experiment of *Ernst Huber* who found the deep sensibility of the face to pass normally after novocain block of the trigeminus. —

fig. 3), and the optic reflexes (e. g. the closing of the eyes in strong light) are also situated at the base of the oblongata (t. b. fig. 3). Similarly collaterals of the anterolateral pain tract enter the nucleus (*Cajal*). Think of the »faces« we make when hurt.

As a consequence, we see that the motor nucleus of the VII, has also acquired as very ventral position, near the above mentioned reflex tracts and also near the decussation of the facial pyramid (py, fig. 3).

At the same time this nucleus has become much larger in accordance with the fact that its muscles have increased largely in extent.

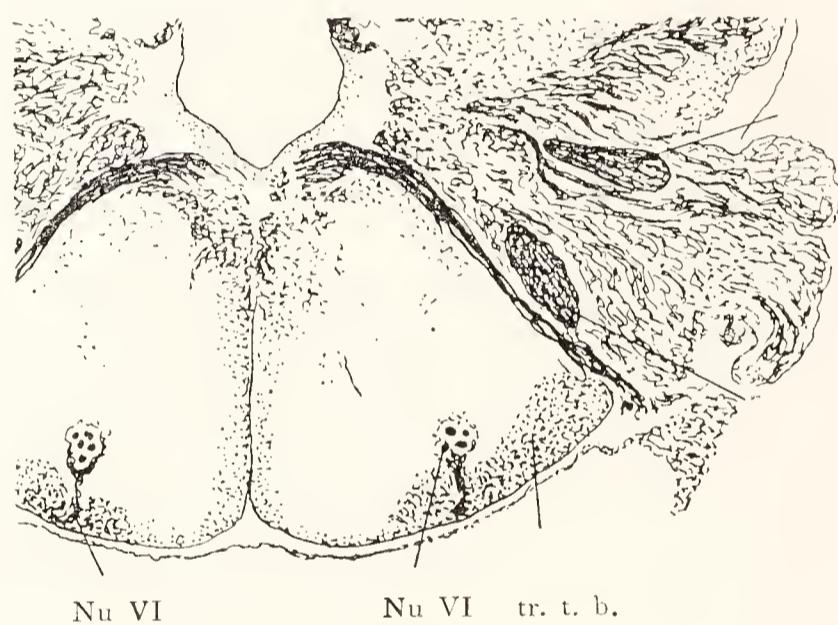


Fig. 4.

Transverse section through the oblongata of a Teleost (Mugil chelo), where the ventral reflex paths of the VI nucleus (tr. t. b.) predominate. Note the small size of the fasc. longit. dorsalis.

Only the sympathetic nuclei of the facialis keep a dorsal position. The salivary center of the sublingual gland (nu. Sa fig. 3) lies near the taste centre (nu. gu.).

As the taste centre influences salivation it is not surprising that the sympathetic cells of salivation remain near this centre (*Yagita and Hayama*).¹⁾

¹⁾ The same holds good for the salivary nucleus of the parotis (IX) which also has a dorsal position in dogs (*Yagita*), not a ventral one as is supposed by *Kohnstamm*.

Similarly the sympathetic centre of lacrymation is located dorsally (*Yagita*).

Another motor nucleus which exhibits a very different place according to the chief reflex system dominating its function, is the *nucl. abducens*.

As is known, the outward rotation of the eye — caused by this nucleus — depends chiefly upon two sorts of impulses — some from the organ of equilibrium, and others from the eye (tectum) itself.

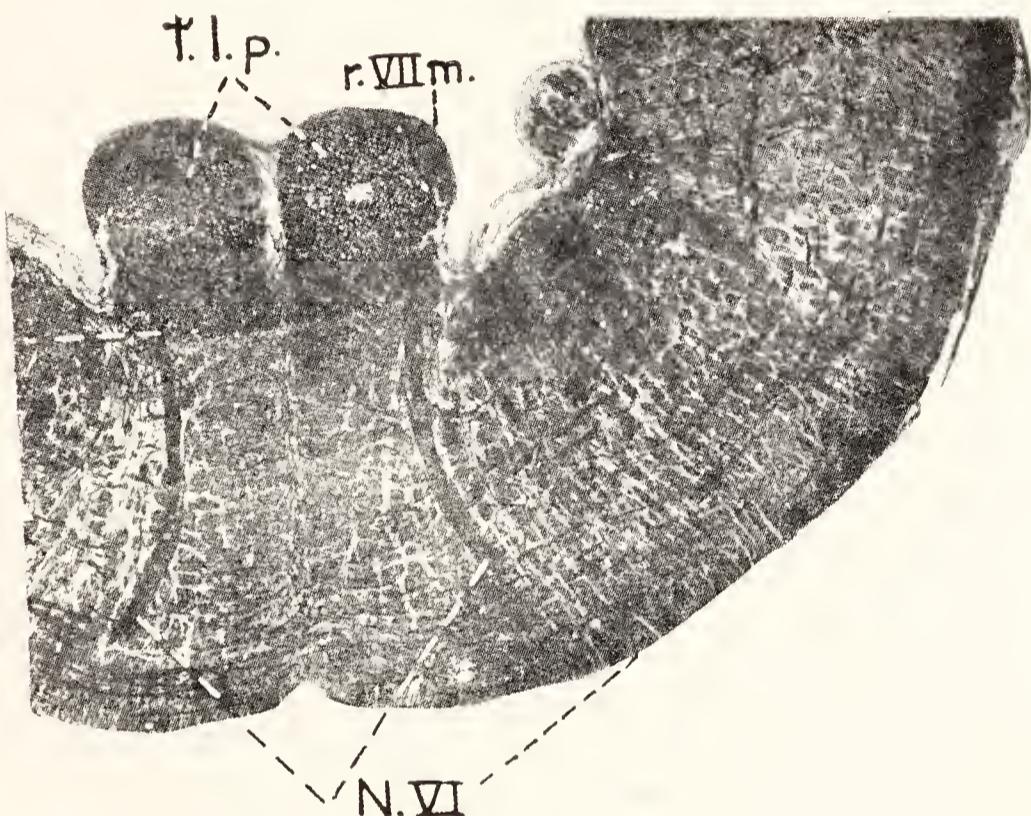


Fig. 5.

Transverse section of the oblongata of a shark. Note the large size of the fasc. longit. posterior (f. l. p.) and the origin of the VI roots, near this fascicle.

Both sets of impulses take their course partly dorsally, partly ventrally in the oblongata.

In those fishes where the dorsal tracts dominate, the abducens nucleus has a dorsal position in the oblongata, and where the ventral reflexpaths dominate, it has a ventral position.

Thus in the fish of which a section is shown in fig. 4 the tr. tecto-bulbaris (tr. t. b.) at the base of the bulb exerts the principal influence upon the abducens nucleus, whereas, in the shark (fig. 5), the dorsal bundle (f. l. p.) exerts the greatest influence.

In both cases the motor nucleus occupies the place corresponding to the strongest reflex tracts.

In mammals and in man the abducens nucleus also has a dorsal position, — only in most cases it lies a little more laterally, under the influence of Deiters' nucleus¹⁾ (fig. 6).

From these examples we see that the structures in the nervous system are arranged according to the impulses that pass through them.

Genu Nervi VII

nucl. triangularis vestib.



Fig. 6.
Transverse section of the oblongata of a rabbit.

It is, however, not merely the impulses that dominate the structures, but the associative relations of the impulses and centres. These associative relations determine the selection.

¹⁾ The accessory abducens nucleus, so carefully studied in various vertebrates by *Tullio Terni*, keeps a more ventrolateral position near the descending trigeminus root, that determines the function of the nictitating membrane, as a protector of the cornea.

Thus in the example of the VII nucleus a motor centre acquires another position when the stimulative relations in the region of the gill arches are changed. It is striking, however, that with an alteration of the sensory relations in the gill region only the motor nuclei of the gill arches and no motor cells of eye-movements change their position.

Why does one group of cells change its position while another does not? The reason for this is, that only this special muscle group (and its proprioceptors) are stimulated simultaneously with the structures in which the stimulative conditions have changed.

Exactly as, in the example of a mental association, the remembrance of a *special* person is associated with a *special* tune, because it was just that person who in our youth played that tune to us, so in the case of material alterations in the nervous system, only simultaneously *associated influences* cause the selection.

It is evident that when the gills are moved, gill sensations and mucous impressions of the animal are simultaneously altered and when the eye moves or the body turns over, other visual and equilibratory impressions arise. Thus changes in special categories of impressions become associated with special movements of the eyes and body.

It is always the simultaneousness of function and impression which causes structural connections. Stimulations which do not occur simultaneously (unless they follow one another *immediately*, occurring *successively*) do not effect each other and thus do not create connections in the nervous system.

Thus it is evident that the same rule which has been known for centuries to act an important part in our mental life also acts an important part in the structure of the nervous system.

In our special case one might say: simultaneous (or immediately successive) stimulations bring about not only mental associations, but also material connections in the nervous system.

This is the principal law of neurobiotaxis, which thus is analogous to the principal law of psychology, already realized by Aristotle.

Since I found this law of neurobiotaxis (1907) it has been frequently confirmed and applied, by myself as well as by others.

I shall discuss a few structural relations, on which it has thrown some light.

Thinking of the proverb: »l'art d'ennuyer c'est raconter tout«, I shall give only short descriptions.

I shall begin with the spinal cord, which in a primitive vertebrate, *Petromyzon*, shows a structure very different from that observed in higher animals and in man.

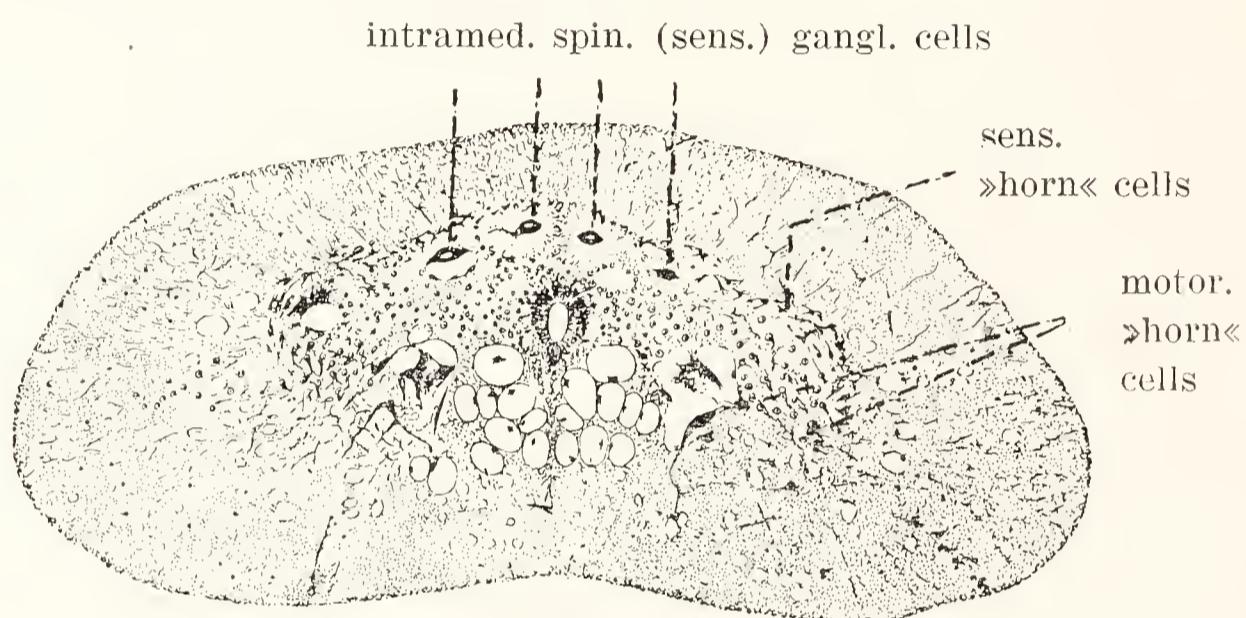


Fig. 7.

Transverse section of the spinal cord of the Lamprey (*Petromyzon*). Only one wing of grey matter is seen on each side of the central canal.

In a transverse section of the cord of the Lamprey (fig. 7) we distinguish a central mass of nerve cells, extending laterally on each side, in one wing only, surrounded by fibre tracts. In each of these wings lie a number of cells, of which the ventral ones are motor cells, the dorsal sensory cells, receiving stimulations from the dorsal or sensory roots.

The motor cells lie very near the sensory cells. Yet these motor centres already receive a number of stimulations from the tracts at the ventral side of the spinal cord, which influence these cells.

Evidently, however, this influence from the basal side is not strong enough to cause a ventral shifting of these cells.

In higher fishes and in all higher vertebrates this is different.

Here a dislocation of the sensory cells in a dorsal direction and a shifting of motor cells in a ventro-lateral direction takes place, the sensory horns being influenced by the dorsal roots, whereas the ventro-lateral tracts that influence the motor nuclei, cause a ventral dislocation of the motor nuclei.

Thus the peculiar arrangement of grey substance in the spi-

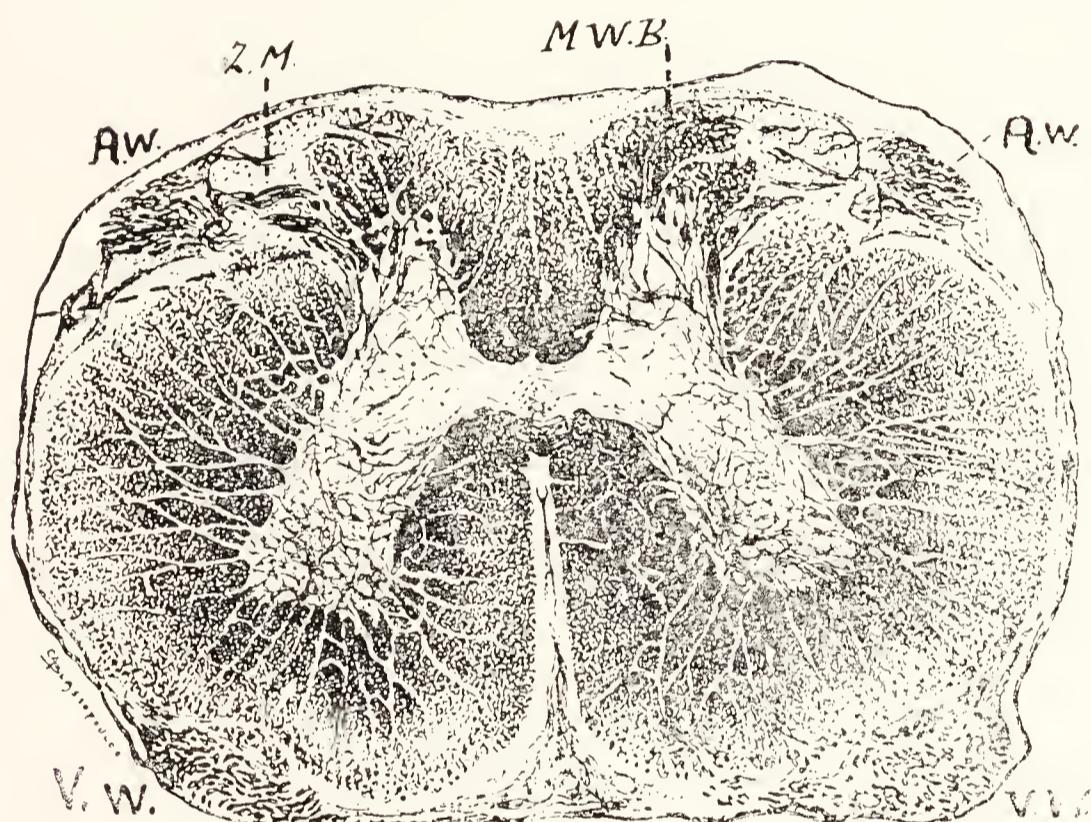


Fig. 8.

Transverse section through the cervical cord of a turtle (Dammonia).

nal cord of a higher animal, is explained by the impulses, reaching the sensory- and motor cells of the cord. *Kraus* and *Weil* even showed that also the shape of the cells in the spinal cord is determined by this process.

Concerning the oblongata, I have already given examples of this process, describing the different positions of the VI and VII nuclei and the course of the V and cutaneous X fibres.

I shall add an example from the acoustic region.

In order to understand this example it should be realized that the acoustic organ in lower animals is very poorly

developed.¹⁾ Most fishes are deaf and in those, which hear the acoustic function is limited to the perception of »Geräusche«.

Real hearing commences (among vertebrates) in Amphibia, and increases in reptiles and birds, to reach its highest development in mammals. Particularly among rodents and carnivora the acoustic apparatus acquires a high degree of development.

This increase in the development of the peripheral acoustic organ has a striking influence upon the acoustic region in the central nervous system (cf. fig. 9 and 10).

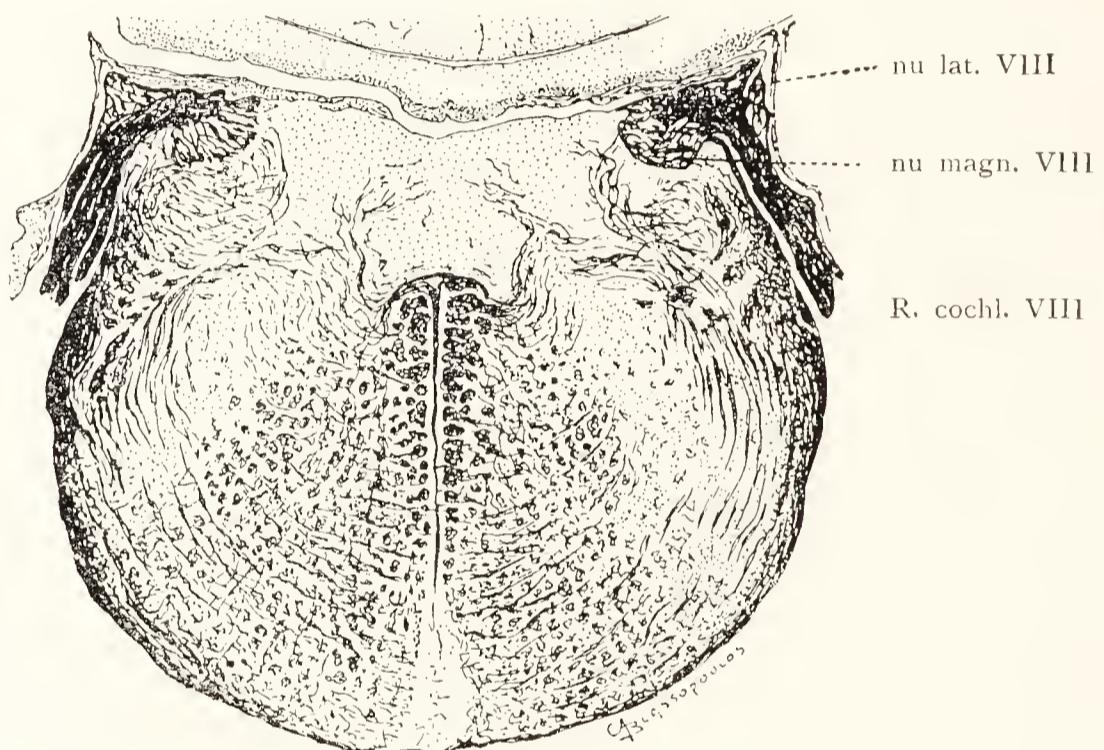


Fig. 9.

Section through the acoustic region of the oblongata of a bird (Pratincola).

In reptiles and birds (fig. 9) both central acoustic nuclei, the *nucl. lateralis* (or *angularis*) and *medialis* (or *magno-cellularis*), lie at the dorsal side of the oblongata.

The cochlear nerve approaches these nuclei from below (see fig. 9).

In mammals, with the enlargement of the cochlea and of the cochlear nerve, these nuclei commence to shift in the direction of the increased nerve. As, however, this nerve approaches the oblongata from below, the originally dorsal centres shift ven-

¹⁾ I. e. the acoustic region in the proper sense of the word. The vestibular and lateral line senses are strongly developed here.

trally and more and more acquire a position near the base of the oblongata.

This migration, already started in the monotremes (*Stokes*) reaches its maximum in rodents, bats, carnivora (fig. 10) and primates.

A similar process of shifting, but in the reverse direction, is observed in the cerebellum. The cerebellar nuclei, originally derived from and connected with the vestibular nuclei, shift more and more dorsally, into the cerebellum itself.

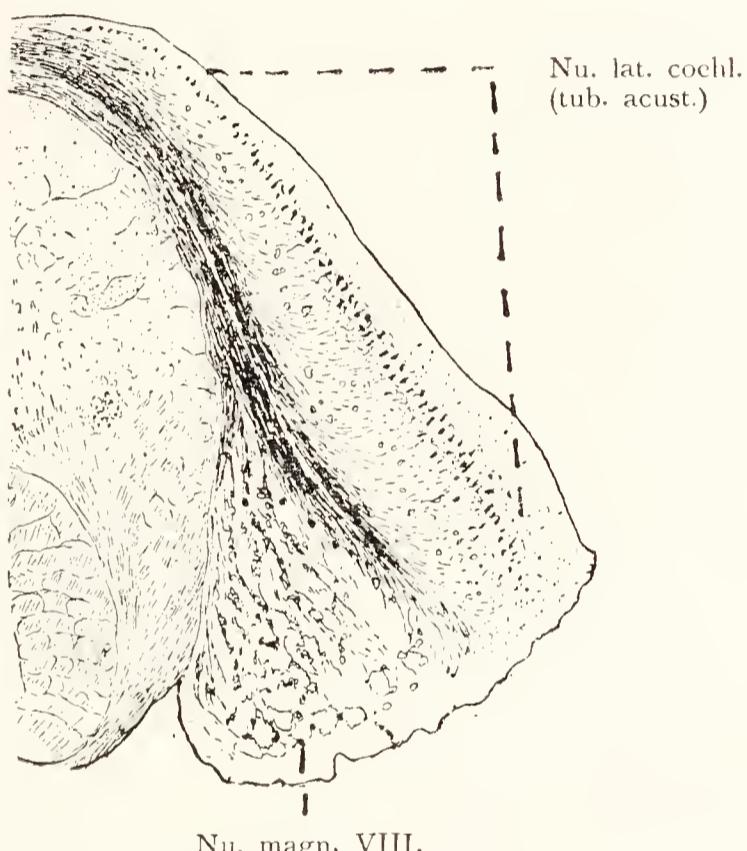


Fig. 10.

Ventral extension of the lateral cochlear nucleus (tuberculum acusticum) and magno-cellular acoustic nucleus (nucl. ventralis) in a cat. After Fuse.

This is due to the fact that the vestibular nuclei of the oblongata receive impulses from the cortex of the cerebellum.¹⁾

So a part of these nuclei, which in lower vertebrates still lie in the dorsal edge of the oblongata, in higher vertebrates shift into the cerebellum forming the nucl. tecti (or fastigii) and the

¹⁾ This is still the case in mammals where Deiters' nucleus and the nucl. rad. vestib. desc. receive fibres from the cerebellar cortex (Hakenbündel).

dentate nucleus. This process already starts in reptiles, but in birds the nuclei mentioned are still contiguous with the vestibular nuclei of the oblongata. Only in the higher mammals they are entirely separated from them, being completely embedded in the white matter of the cerebellum.

With the increase of the cerebellar cortex and of the stimulations radiating from the *Purkinje* cells, the nuclei shift more and more in the direction of that cortex, so that the nucl. tecti which is chiefly connected with the cortex of the anterior lobe (*van Valkenburg*) extends more frontally than the dentate nucleus that lies nearer the cerebellar hemispheres, extending sometimes a separate part into the flocculus (rabbit).

Also in the mid- and 'tweenbrain topographic changes resulting from special stimulative relations are found, as, for instance, the outgrowth of the valvula cerebelli under the tectum, the outgrowth of the torus longitudinalis tecti, the ventral elongation of the so-called nucl. anterior thalami of teleosts to the hypothalamus as nucleus rotundus, etc..

In order to explain these facts I should, however, have to enter into the special hodology of these animals, which would carry me too far here. I shall only say a few words about the visual system because this system clearly shows how important simultaneous stimulations are in determining the course of fibres, and also in altering their course.

This is a very difficult subject, as I have to start with the remarkable fact of the total decussation of the optic nerves in lower vertebrates.

To this decussation *Ramon y Cajal* has given a teleological explanation, based upon to necessity that the part of the panorama observed by each eye, is projected upon the midbrain,¹⁾ in such a way, that the part of the projection localized to one eye and to the corresponding half of the midbrain is linked up in a natural way to the part projected in the other eye and upon the other half of the roof of the midbrain.

¹⁾ In most teleosts the main projection is upon the midbrain; only some temporal retina fibres (*Lubsen*) end in the gangl. geniculatum laterale, which for the rest may be chiefly connected with optic collaterals.

The scheme drawn in fig. 11 shows that this necessity is met by the total decussation of the optic nerves and not by a homolateral course of the optic fibers.

A merely teleological explanation, however, gives little satisfaction, as the question remains: if it be necessary for the natural relation of perception that there be a total crossing, how

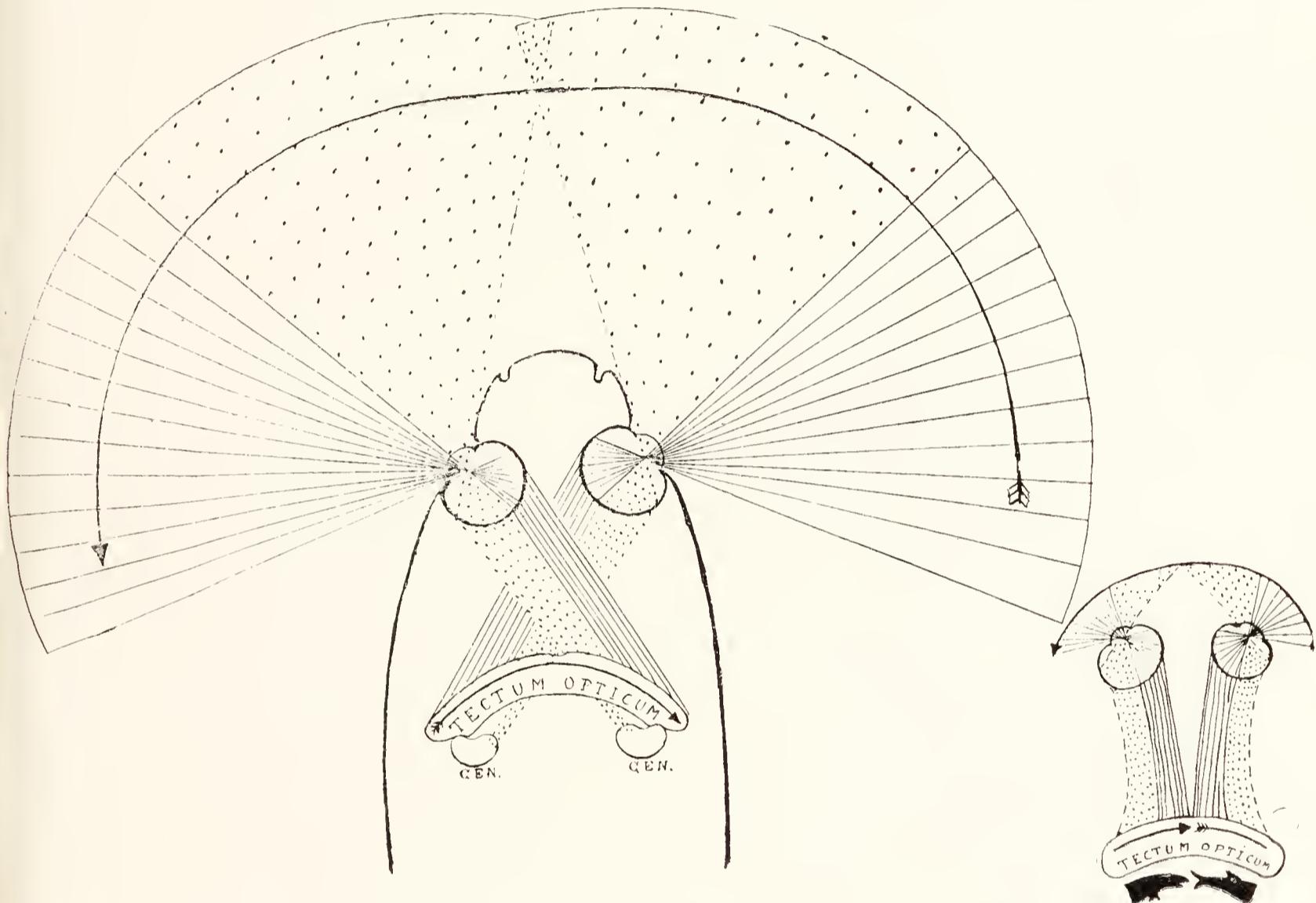


Fig. 11.

Illustrating *Cajal's* explanation of the total optic decussation in fishes. The small figure at the right shows the lack of natural combination between images of the two eyes if the nerves did not decussate (especially if the arrow be replaced by a fish which appears in the visual fields).

is this relation realised? By which intrinsic qualities of the nervous system are the fibres thus arranged?

That the endings of the optic fibres on the midbrain really are such as is required by the theory of *Cajal*, is evident from investigations of *Zeeman* and *Lubsen*, who, did not published their results but communicated them to me.

Is it not possible, however, to explain this arrangement by the facts of neurobiotaxis and thus give a causal instead of a teleological explanation of this relation? We might at any rate try to do so.

When regarding the visual relations in fishes we must take it for granted that the eyes of most lower vertebrates — where the total decussation occurs — are located laterally in the head, looking sideways and not, as with us, forward. — Neither is there any active convergence in fishes.

If we now follow the (reverse) projection of the panorama upon the retina of these eyes and mark out its further projection upon the midbrain with an arrow (as *Cajal* did), we then notice that this arrow is only completed in an exact (though reverse) way, when the optic nerves of both eyes decussate and not when each of these nerves ends on the same side. —

This arrangement can, however, also be explained in the following, way by the law of simultaneous association.

In the whole panorama, there is only one section that may be seen by both eyes simultaneously, viz. the middle of the panorama, which is projected upon the utmost temporal parts of each retina (c. f. fig. 11). —

If, however, the area in the middle of the panorama is seen by both eyes simultaneously, the utmost temporal retina parts, which are simultaneously stimulated by this middle-part, should join centrally according to the law of neurobiotaxis, i. e. they should meet in the middle of the roof of the midbrain, as they do.

The degree of associate collaboration for the visual fields is the smaller the more they are placed further away from each other¹⁾ and we see in fig. 11 that centrally these fibers are projected far away from each other.

In other words, the useful relation emphasized by *Cajal* and proved to exist by *Zeeman's* and *Lubsen's* experiments need not

¹⁾ So the small figure with the uncrossed optic nerves is neurobiotactilly impossible because here the extreme points, which never are seen simultaneously by both eyes are drawn joining each other.

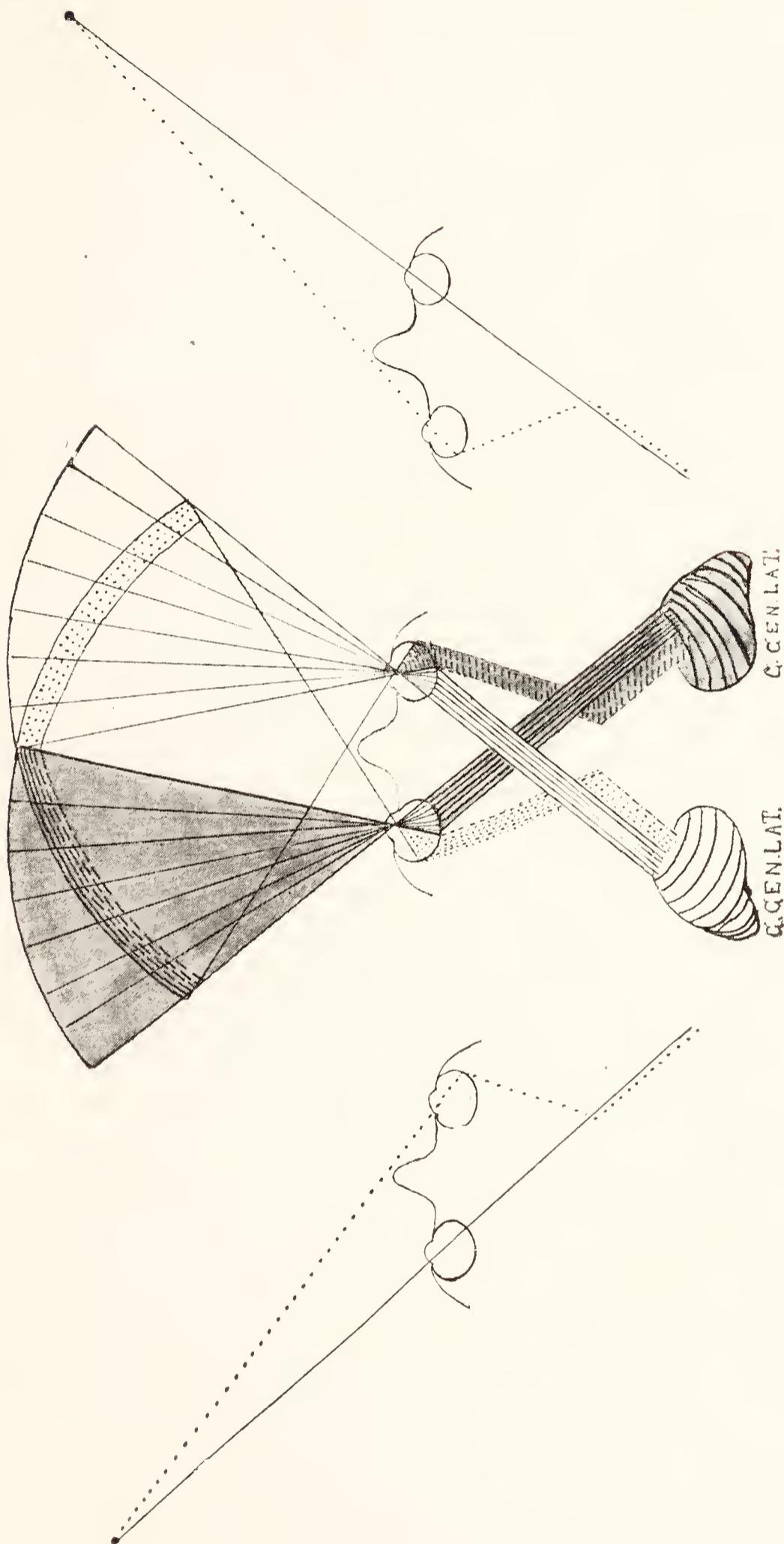


Fig. 12.
Scheme showing the temporo-nasal collaboration of the two retinae of man in convergent frontal vision (middle) and non convergent lateral vision (side figures). Temporal retina fibres dotted and nasal retina fibres fully drawn.

be explained teleologically, but may also be explained causally by the same neurobiotactic principle as met with everywhere in the nervous system, and which has also been adopted by the above mentioned authors.

In favour of this neurobiotactic explanation of optic nerve relations is the fact that it also, and even more obviously, holds good for the relation in mammals, where, with the frontal position and convergenece of the eyes, the total decussation has changed into a semidecussation.

A frontal position with convergent eye-axes running through the maculae as centres of convergent vision, includes a much larger projection of the visual field on the retinae of *both eyes*, as appears from fig. 12 (middle).

We see in this figure that this position of the eyes causes not only both central retinal parts (maculae) to collaborate simultaneously in the perception of the central part of the panorama, but that also the temporal retinal field of one eye collaborates with the nasal retinal half of the other in observing lateral parts of the panorama (see also the side figures of fig. 12).

As a consequence of this overlapping of visual fields and the simultaniety of the temporal retinal function of one eye with the nasal retinal function of the other, we may expect not only the macular fibres of both eyes to collaborate in the brain, but also the temporal fibres of one eye to end together with the nasal fibres of the other. And this is indeed the case, — as is well known.

Consequently the optic fibres in mammals and man become partially homolateral, on account of the fact that the temporal half of the retina of one eye functions simultaneously with the nasal projection of the other.

The temporal fibres of one eye join the nasal fibres of the other, on account of simultaneous stimulation.

As, however, the nasal half of the retina keeps its old homolateral function, whereas the temporal half of the retinal changes its function, from a homolateral to a heterolateral one (with regard to the midline of the body), there is no reason for the

nasal retinal fibres to alter their original course, but only for the temporal fibres, as really occurs.

Better than words figure 12 shows the cause of this relation; here we see that the course of the optic fibres in man is in perfect accordance with the neurobiotactic law of the influence of simultaneous stimulations.

From the facts and causes given here, interesting deductions may be drawn relating to the development and significance of the gangl. geniculatum¹⁾ and the topographic change of the centre of exact vision from the lateral to medial side in the temporal retinal field through the series of vertebrates. For this I have, however, no time in this short review.

I prefer to mention another example, where bilateral simultaneous impulses cause a central union of bilateral projections by partial decussation, viz. the remarkable central connections of the organs of equilibrium (statocysts) in an invertebrate (Pterotrachea) as described by *Tschachotin* (fig. 13).

As the figure shows, here also a partial crossing of central fibres occurs and this too is easily explained by neurobiotaxis.

In both statocysts the statolith, which stimulates the macula (M) as well as the neighbouring hair cells, presses upon the right wall of both statocysts, if the animal turns over to the right side, i. e. stimulates the outer half of one statocyst, while it stimulates the inner half of the other.

Neurobiotactically this implies that the fibres of the outer half of one statocyst must centrally join the fibres of the inner half of the other statocyst, and this actually occurs.

Consequently the central connections become such, that the nerves of both statocysts exhibit a static semi-decussation.

As with the visual semi-decussation this has the useful effect that both statocysts collaborate very closely in one ganglion at every change in the position of the animal and consequently the animal is more quickly stimulated to correct its position.

Thus here also we have a teleological consequence, causally explained.

¹⁾ For these I refer to the investigations of *Brouwer* and *Zeeman*.

I shall now mention some examples of neurobiotaxis in the development of the *forebrain*, which, still small in primitive vertebrates, and increasing considerably in the higher ones, finally develops to the large forebrain mantle of man, the seat of our highest functions (cf. fig. 15). —

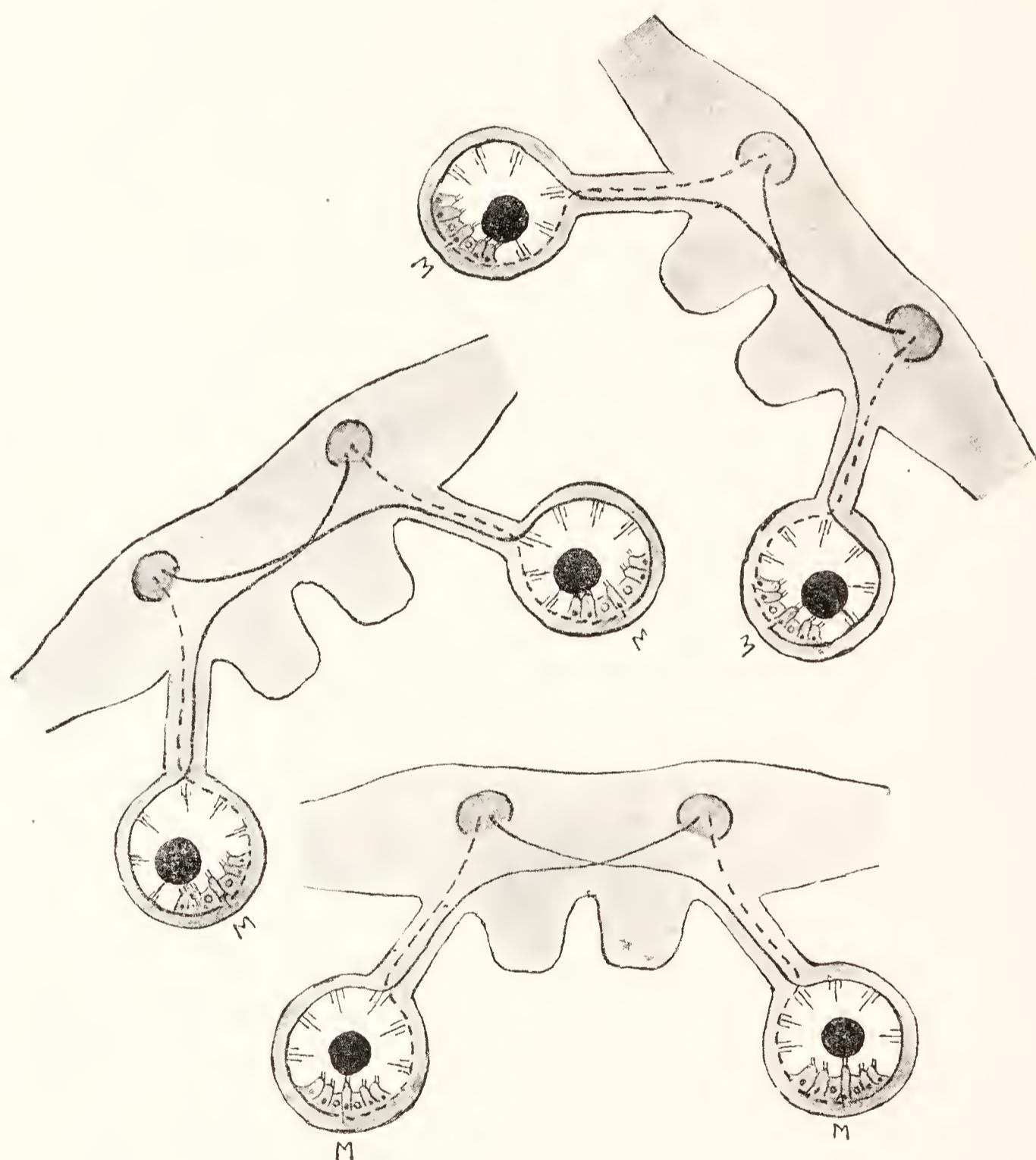


Fig. 13.

Partial decussation of the statocyst fibres of *Pterotrachea*, causing the simultaneously stimulated outer half of one and inner half of the other statocyst to be projected centrally in one ganglion.

Before dealing with the causal influences, which determine this increase, I want to mention that the forebrain in its first organisation develops under the influence of the organs of smell.

While these organs are paired in all vertebrates, the condition is different in the ancestral form: *Amphioxus*.

In this animal one finds an unpaired organ of smell¹⁾ from which nerve fibres grow out into the frontal wall of the brain

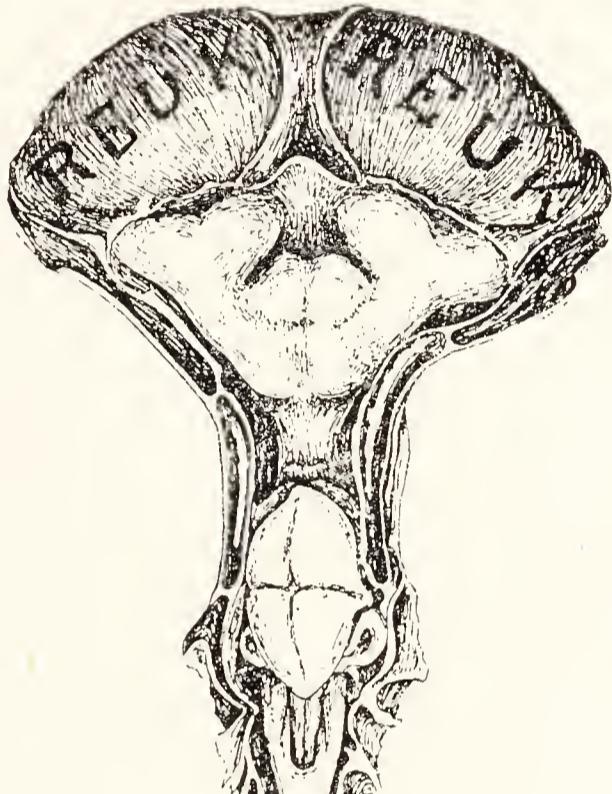


Fig. 14.

Bilateral outgrowth of the telencephalon to the bilateral olfactory placodes (Reuk) in a shark.

vesicle, and this consequently keeps its original impair character.

In all higher animals (e. g. the sharks, fig. 14), two olfactory organs are found, one on each side of the head.²⁾

In accordance herewith, and as a neurobiotactic consequence, the originally impair forebrain forms paired protrusions in the direction of these olfactory organs (the lobi olfactorii).

That the outgrowth of the forebrain in the direction of the

¹⁾ The olfactory character of this organ in *Amphioxus* has even been doubted recently by *Franz*.

²⁾ A third, impaired one, still present in the lamprey, disappears, being absorbed in the organisation of the hypophysis (*Woerdeman*).

olfactory placodes is really determined by those placodes, is demonstrated by the experiments of *Burr*, who cut out the rudiment of those placodes in young larvae of amphibia and inserted them again in another place on the head. Developing in the new place, they caused another part of the brain wall to grow in their direction.

Besides, we know of pathological cases in man where the paired olfactory sense epithelium has not developed.

Such cases of *arrhinencephaly* are described by *Riese* and by *de Jong*. In these cases also the frontal part of the forebrain had not grown out bilaterally in a frontal direction but frontally remained unpaired.¹⁾

Thus it is evident phylogenetically as well as experimentally and pathologically, that the paired evaginations forming the secondary forebrain (telencephalon) depend on neurobiotactic influences of the paired olfactory placodes.

In lower vertebrates, the forebrain is chiefly olfactory²⁾ in character. Not till later in phylogeny do many other impressions join the telencephalon, causing a considerable enlargement of this region, especially in mammals, where nearly all sensory and motor centres are associated with it.

An idea of this increase is given in fig. 15, where the brain of a fish, a reptile, a bird, a marsupial, a dog, a primate, and a man (Indian) are represented on the same scale. From this it is obvious that the forebrain of a bony fish is even smaller than its midbrain.

We should now consider the question: why is it that the forebrain becomes the centre of so many associations and why does not the midbrain develop into the general associative region of the nervous system?

This question is the more urgent as in lower animals the midbrain has such an important function, not merely as a visual centre, but also as a centre of primitive sensory im-

¹⁾ That the occipital parts of the forebrain develop bilaterally in such cases must be attributed the fact that in man the projection of other functions is also paired.

²⁾ Not exclusively, however.

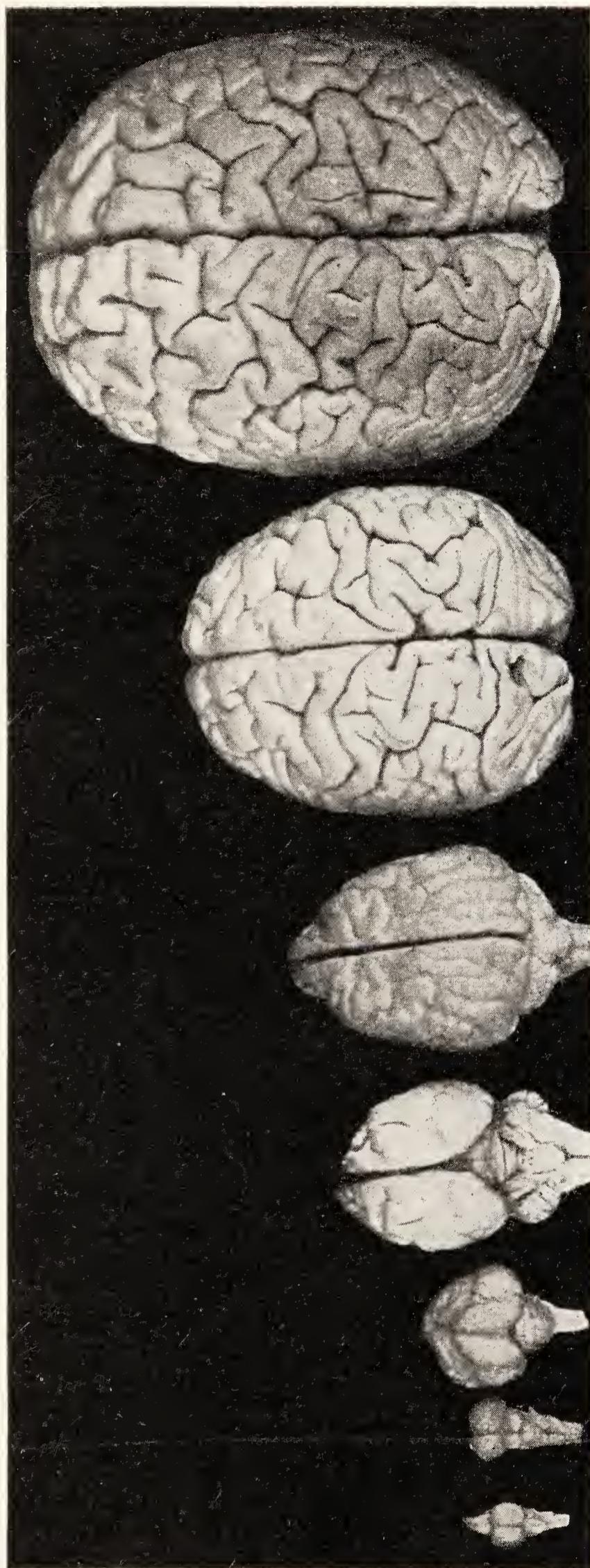


Fig. 15.
Comparison of the development of the forebrain in a freshwater fish (*Esox*), the crocodile, a bird,
a marsupial, a dog, a chimpanzee and man.

pressions, primitive muscle sense and impressions of equilibrium, while the forebrain is mainly olfactory here.

It is not so easy to answer the question why the general associative centre of the nervous system does not develop in the midbrain.

Perhaps the following considerations may throw some light upon this question.

The projections connected with the midbrain, particularly in fishes, all have the characteristic of primitive sensations (protopathic sensations, *Head*, dyscritic sensations, *Parsons*¹), that means they are sensations of little discriminative value mostly belonging to the class called by *Sherrington* nociceptive sensations, which result principally in negative reflexes: avoiding reflexes, correcting movements of the body or the eyes.

We know, however, that *smell*, which is localized in the forebrain, is a sense of high discriminative value by which even man (in whom it is relatively little developed) may recognize quantities of some odorific substances 250 times smaller than can be detected by spectral analysis (*Zwaardemaker*).

Smell can even discern ethyl alcohol in a dilution 25000 smaller than observed by taste (*Parker*).

When this is the case with man, how much stronger and of how much greater explorative value is the sense of smell of lower animals that scent objects miles away.

It is only in higher animals that other sense organs develop a similar degree of discriminative and explorative value.

The higher discriminative development of other organs begins with the sense of touch in reptiles by a refinement of the sense of the head, especially the *orsal sense* (*Kappers*). This is located centrally in the frontal sensory V nucleus and is projected not only upon the midbrain, but chiefly on the forebrain, partially indirectly (thalamus) partially directly (principally in birds).

In the forebrain, however, this new discriminative sense is associated with olfactory stimulations.

The impulses, which thus join the rhinencephalon are again

¹) An introduction to the theory of perception. Cambridge University Press, 1927.

discriminative impulses in case cutaneous and proprioceptive discriminations of the mouth, nose and head.

Particularly in birds this association is very striking (Tr. quinto-frontalis, *Wallenberg*). — It is, however, looking at it from a neurobiotactical point of view, not strange that this discriminative sense becomes associated with smell.

When searching for food terrestrial animals, especially mammals, use smell simultaneously with discriminative impulses of the mouth and nose, while the search for food in the case of fishes in water does not cause nearly as much rubbing of the head and mouth.

This also explains the fact that with terrestrial life the sensory organs of touch of the head increase, while taste decreases. In this respect also the sinus hairs of mammals act a large part.¹⁾

It is not surprising that this explorative sense, of the V, should join the olfactory region and consequently the forebrain, which thus becomes an associative region of still higher *discriminative significance*²⁾ in the exploration for food (*sniffing*).

With mammals, the anterior extremities become also involved in the exploration of food, as is evident with rabbits, moles, and some carnivora. In connection herewith it is not strange that next to and above sensibility of the head the sensibility of the forelegs is projected upon the forebrain, followed only later in phylogeny by the projection of the trunk and hindlegs.

Thus in these projections on the mantle a peculiarity appears which may also be explained by associative relations.

¹⁾ See *Kappers* Vergleichende Anatomie des Zentral Nervensystems etc., Vol. I Bohn, Haarlem, 1920, p. 335—336. — The great influence of the sinus hairs on the trigeminus also appears also from the fact discovered by *Ernst Huber* and *Hughson* that their localization and development even determines the place of the cranial foraminae of this nerve.

²⁾ The increase of the forebrain as a centre of discriminative associations, is seen also in connection with vision, as the lower visual reflexes (observed by the peripheral retinal fields) remain located, also in mammals to the midbrain, whereas the discriminative centre of the retina, also the macula — is projected on the forebrain.

It is well known that the projection of cutaneous and deeper sensibility upon the cortex is such that the sensibility of the head is located ventrally, near the olfactory lobes, and that of the hindlegs dorsally (*Cushing, v. Valkenburg*).

The projection thus is the contrary to the position of an erect body. This, however, is not surprising from the stand-point of neurobiotaxis, since we know that the sensibility of the head is the first discriminative sense associated with smell.

We may expect therefore that this projection immediately borders on the smell-area. Since, however, smell is primarily located to the ventral side of the forebrain, head sensibility can be projected only above it, followed by the projection of the forelegs, which is the most closely associated with that of the head. After this follow the projections of the body and of the hindlegs.

The reverse projection of the body upon the cortex thus has the useful effect that the projection of the oral sense (nose and mouth) is nearest to that of smell.

Here also, however, we see that this useful effect need not be explained teleologically, but that it is caused by the association of simultaneous stimulations, which do not only act a large part in the development of our mental life, but are just as well found in the structural phenomenon of neurobiotaxis.

Many other examples of neurobiotaxis might still be mentioned, but I fear that I have already given too many details in this one hour.

I hope, however, that, when these details have been forgotten, two cardinal points may be remembered:

- 1o. That the mental law of association may also be observed in the phenomena of neurobiotaxis.
- 2o. That the teleologic character of the intrinsic structure of the brain, coincides with neurobiotactic causality.

THE CORPUS STRIATUM, ITS PHYLOGENETIC AND ONTOGENETIC DEVELOPMENT AND FUNCTIONS

Before dealing with the corpus striatum itself I must call attention to the general subdivision of the neural tube, as this is of fundamental importance in order to understand the region where the striatum arises.

It is well-known that the median lines of junction, the floorplate and roofplate of this tube are different in character, the floorplate being joined *ab origine*, whereas the dorsal junction forming the roofplate only arises when the tube closes, and is thus a *secondary* junction. As we know this closure is first established about the middle of the tube and grows gradually forwards and backwards. Both roof- and floorplate are thin.

In the thicker lateral walls of the embryonic tube a sulcus may be observed especially in the spinal cord and the oblongata: the *sulcus limitans of His*. It divides the lateral walls into two regions, a dorsal or *alar region*, and a ventral or *basal region*. —

It has been a matter of some discussion how far the *floorplate*, the primary junction of the tube, extends frontally. Researches made by *Kingsbury*, *Kingsbury* and *Adelman* and by *Burr*, seem to have settled this problem. The floorplate, according to these authors, does not extend beyond the mammillary region of the brain, but ends in what is generally called the *tuber posterius* (the backwall of the infundibulum). This conclusion is experimentally confirmed by *Bok*.¹⁾

¹⁾ This author put a hair in the open neural tube of a frog and then allowed the tube to continue its growth. Later he found it sticking out anteriorly from the tuber posterius, the frontal part having closed secondarily around it.

All the rest of the brain possesses only a secondary joining which extends from the whole dorsal region of the spinal cord, over the oblongata, midbrain and primitive prosencephalon, bending anteriorly over what is generally called the lamina terminalis (which consequently is not a primitive junction) into the bottom of the hypothalamus.

It is in the frontal region of this line of junction that the last closure takes place. The exact position of this neuroporus anterior, however, does not seem to be constant. In Mammals it lies (*van den Brock, J. P. Hill*) in front of the anterior commis-

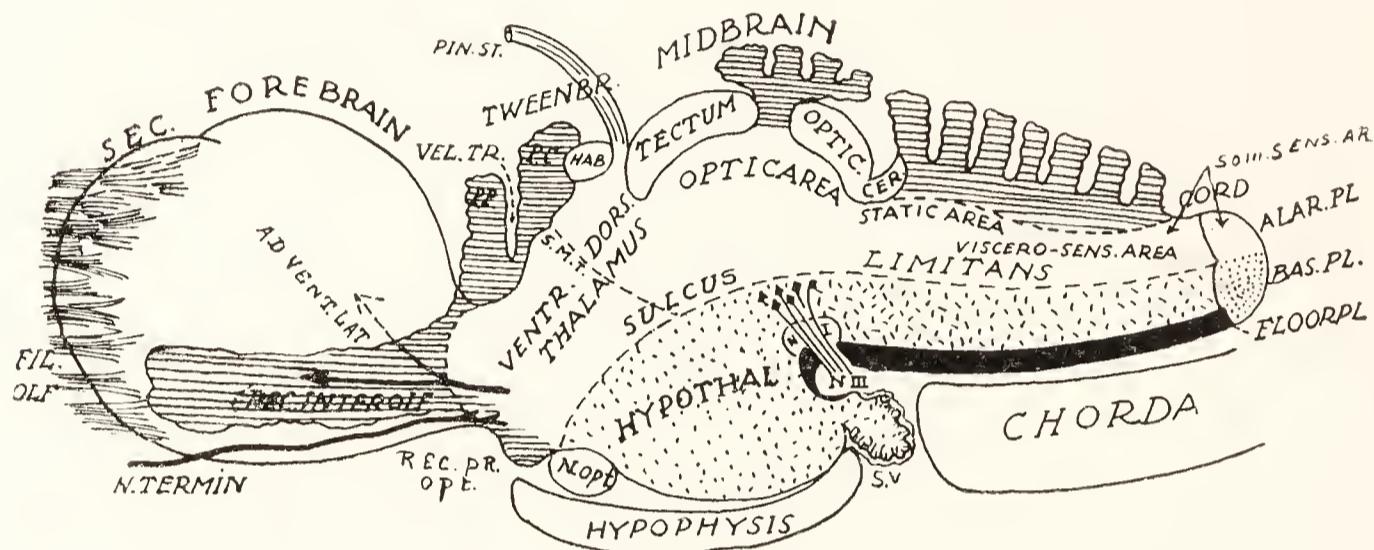


Fig. 1.
Schematic representation of the chief subdivisions of the brain in a primitive fish.

N. termin = Nervus terminalis (failing in the lamprey, but present in all other fishes). rec. pr. opt. = recessus praopticus.

s. v. = saccus vasculosus (failing in the lamprey, but present in all other fishes).

pin. st. = pineal stalk.

p. p. = paraphysis.

p. c. = parencephalon.

n. I = nucl. interpeduncularis.

sure, in sharks, reptiles and birds (*r. Wyhe*) lower down and further back in the region of the optic chiasm. Consequently the position of the neuroporus anterior is not such a typical brainmark as was formerly believed. The *sulcus limitans*, on the other hand, is a very important brainmark, as it indicates the limit

between the sensory (alar) and motor (basal) region of the neural tube.

While the alar or sensory plate of the tube increases in size frontally, the motor or basal plate ends at the preoptic recess (*His, Johnston, Brailey*), or even more backward (*v. Schulte, Tilney, Kingsbury*).

The sulcus limitans indicates the position of the sympathetic



Fig. 2.
Nucleus praopticus magnocellularis of *Lota lota*.

centres (the intermedio-lateral nuclei in the cord, the dorsal vagus nuclei, the salivary centres and lacrymal centres in the bulb, the Edinger-Westphal nuclei of the internal eye-muscles in the mid-brain). Other sympathetic centers are found at the place, where the sulcus bends down into the optic recess near the tuber cinereum. This frontal sympathetic centre of the 'tweenbrain is very conspicuous in fishes, namely in Teleosts.

In these animals we find near the praoptic recess a mass of

large cells (fig. 2) the *nucl. magnocellularis praopticus* (or *nucl. supra-chiasmaticus*), which apparently is sympathetic in character, since its neurites run backward in the bottom of the hypothalamus as the *tr. praethalamo-hypophyseos et saccularis* (*Johnston*), ending among the glandular cells (*N. Holmgren*) of the hypophysis, and the bloodvessels of the *saccus vasculosus* (*Dammerman*).

The area where the cells of origin of this tract lie, also receive fibres from the *N. terminalis*, which includes sympathetic neurones in many animals. This also is in favour of the sympathetic function of this region. Similar cells are to be found where the above mentioned tract enters the cerebral stalk of the hypophysis (*nucl. hypothalami ventralis*) and analogous cells lie between both these groups (*nucl. hypothalami lateralis*). The *nucl. hypothalami* (or *tuberis*) *ventralis* is particularly large in *Belone* (fig. 3 at X).

The same cellgroups are found in dogs, cats and man, where they are of great influence (*Camus* and *Roussy*) on the hypophyseal function, their destruction causing changes in the blood-pressure and diabetes insipidus; lesions of this region may even cause death from shock (*Felding*).

The appearance of these cells corresponds with their sympathetic character as I found them to be more or less chromaffin and possessing sometimes more than one nucleus.

I found them richly provided with bloodvessels, which makes it possible that they are more apt than other cells to act upon the hormonistic elements of the blood. —

Moreover in cats the sympathetic character of this region has been proved experimentally by *Karplus* and *Kreidl*, who showed its influence upon the bloodpressure and the pupils, via the thoracic sympathetic system.

I mention these facts because they show that the place where the *sulcus limitans* ends is, like the rest of this sulcus, a place of predilection for central autonomic nuclei.

Immediately in front of this place the *palaeostriatum* arises, the primordium of which lies near the cells around the preoptic

recess (fig. 5). I shall return to this point when I discuss the function of the striatum.

The morphology and phylogenetic development of this body is best studied by starting with the *forebrain* of *Amphibia*, which is a prototype of the forebrain of higher vertebrates.

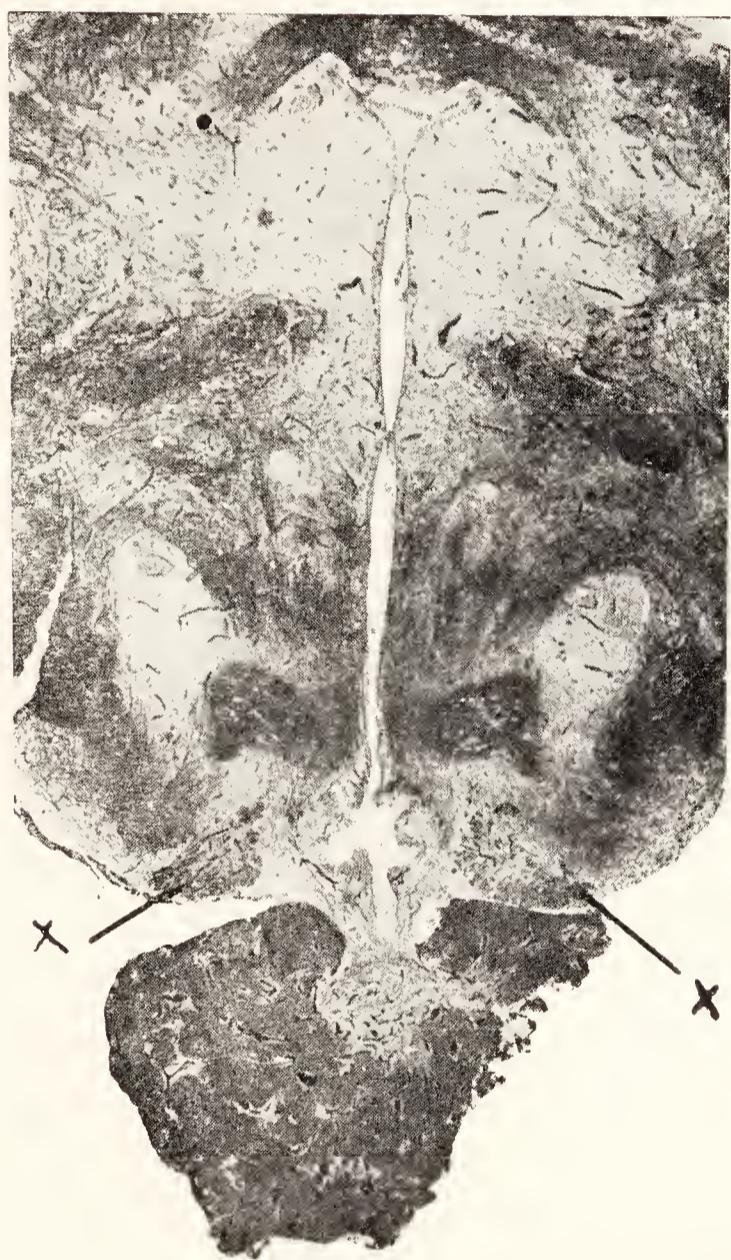


Fig. 3.

Transverse section of the infundibular region of *Belone belone*. Nuclei hypothalami ventrales (X X).

In my following lecture I shall discuss the forebrain mantle of the frog: the palaeo- and archicortex.

I shall now deal with the ventral or striatal region of the frog, because this provides the basis for understanding the development of the striatal complex in Reptiles, Birds and Mammals.

The arrangement of the striatal complex in *Amphilia* is very simple. Two parts may be distinguished, an *epistriatum* and a *palaeostriatum*. They do not seem to be related. The *epistriatum* is a ventricular thickening of the lateral brainwall, receiving olfactory tract fibres (Herrick¹).

It already appears a good distance in front of the foramen

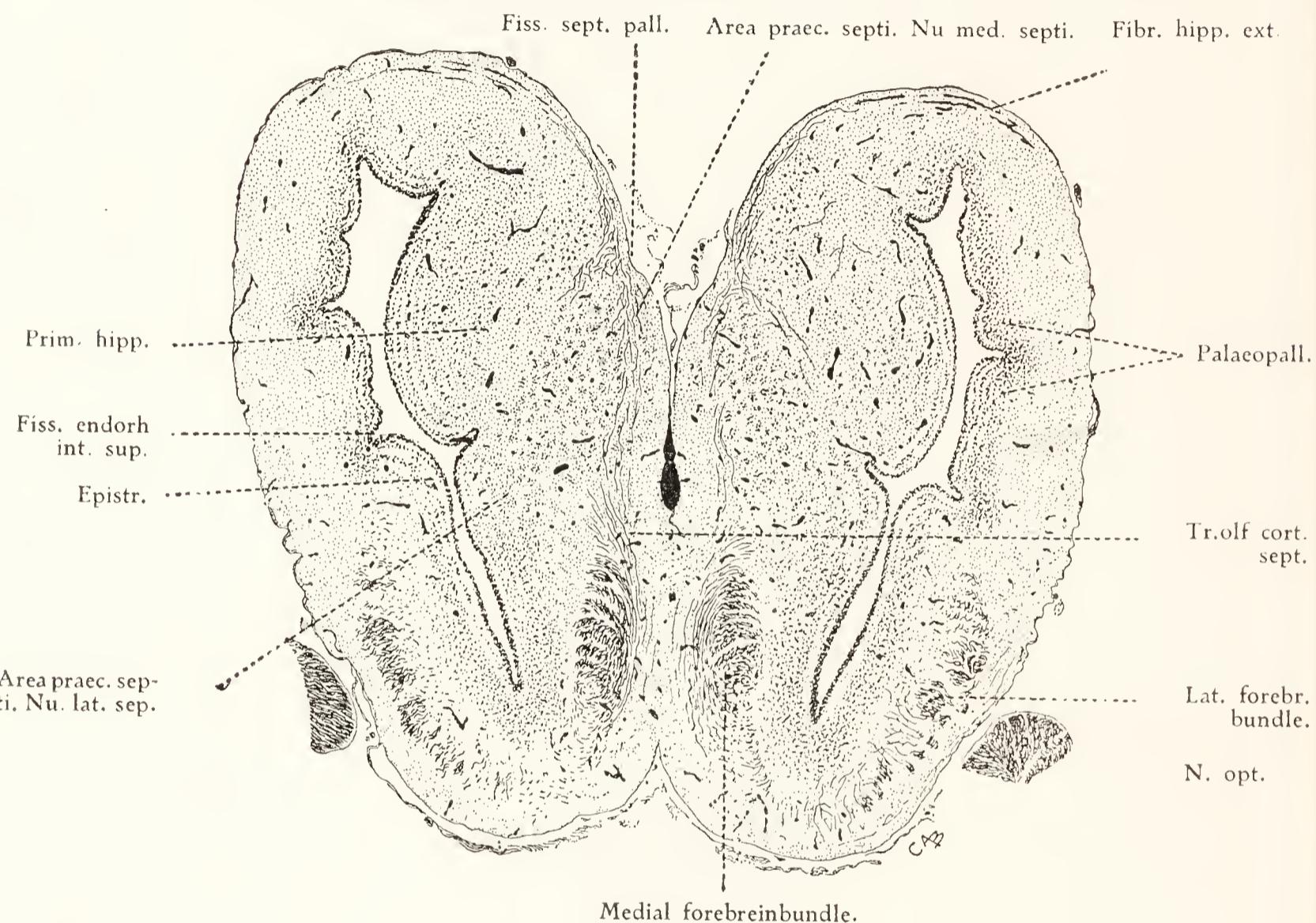


Fig. 4.

Section through the hemispheres of *Rana mugiens* at the level of greatest development of the epistriatum.

Monroi (fig. 4) and, diminishing in size (fig. 5), extends backward, gradually disappearing into the lateral wall.

The *palaeostriatum* develops in the basis of the fore-brain more ventrally and caudally (fig. 5), near the foramen Monroi.

¹) Herrick found that the fibres of the accessory olfactory bulb — a special part of the bulbar formation in frogs — ends here. I am able to confirm this.

The palaeostriatum receives impulses from the lower thalamus (peduncular nuclei). It contains large cells, the neurites of which form the descending striohypothalamic tract, running in the lateral peduncle of the forebrain (fig. 5). In this bundle cells are found which reinforce the tract and which are more or less

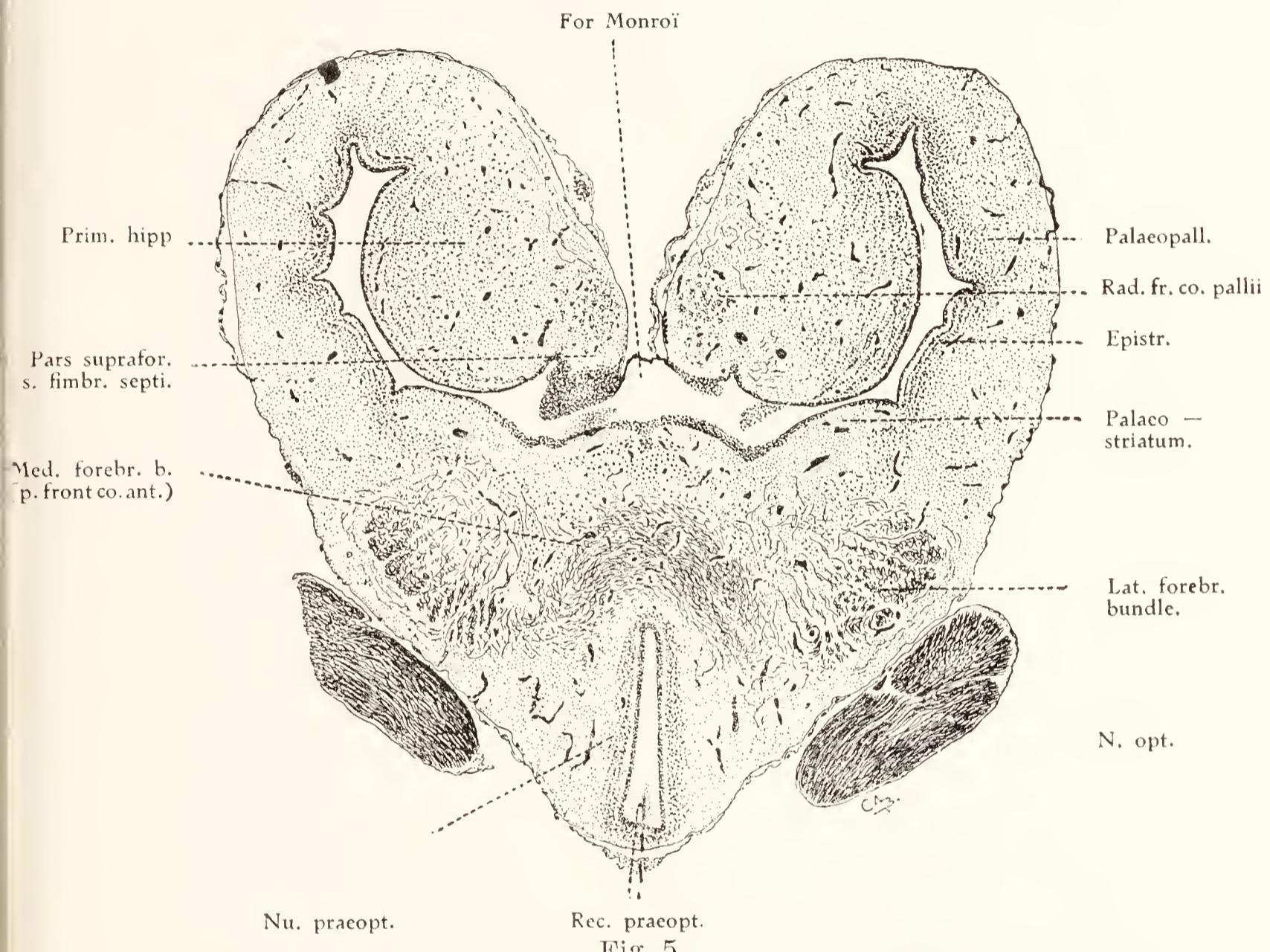


Fig. 5.

Transverse section of the forebrain of *Rana mugiens* at the level of the foramen of Monro, the preoptic recess and the palaeostriatum.

contiguous with the cells of the palaeostriatum. These cells are the primordium of the substantia nigra of mammals.

In *reptiles* the striatal complex, and, in connection with it, the dorsal thalamus, shows a progressive development. I shall illustrate this by photo's of *Varanus salvator* (for the Alligator see *Crosby*).

Both the striatal nuclei described in frogs are found in reptiles, but to both of them other striatal territories have been added. The epistriatum as it is found in *Amphibia* is in *Reptilia* more or less represented by a lateral mass of cells lying a short distance behind the insertion of the olfactory stalk and generally referred to as the *lateral olfactory nucleus of Crosby*. It receives olfactory tract (mitral cell) fibres as does the epistriatum of the frog — though most of these end in the palaeocortex (as they also do in frogs). This small centre is, however, entirely hidden in Reptiles by the addition of a large *secondary epistriatum* or *archistriatum*, which develops from the lateral wall of the hemisphere (partly from the piriform cortex) behind the nucleus olfactorius lateralis and which does *not* receive olfactory tract fibres, but fibres arising in the (olfactory) palaeo-cortex. This tract was called by *Edinger* tr. *cortico-epistriaticus*. A still better name is *tr. cortico-archistriaticus* (fig. 6). The archistriatum in which it ends posteriorly grows out caudally to a large mass, which forms the most caudal part of the whole striatal complex, reaching the hindpole of the mantle, just as its mammalian homologue, the *amygdala*, does.

In Lizards the amygdala is relatively larger than in mammals, forming the caudal half of the whole intraventricular complex.

The archistriata of both sides are connected by the commissura archistriatica. From the archistriatum an efferent tract (described by *William Herman*) runs to the hypothalamus and mesencephalon.¹⁾

Ventro-medially to the archistriatum, directly in front of the foramen Monroi, lies the *palaeo-striatum* or basal nucleus (fig. 7), consisting of large efferent neurones. This palaeo-striatum is relatively small and is covered by the archistriatum. It is sometimes delimited by a large bloodvessel (*Elliot Smith*).

On top of the palaeostriatum and medial to the amygdala

¹⁾ This tract is homologous to *Wallenbergs* tr. *occipito-mesencephalicus* in birds, which there also arises from the archistriatum (A. Hermann).

(fig. 7) lies the third and most important component of the striatal complex, the *neostriatum* (fig. 6, 7 and 8), the frontal extension of which stretches far beyond the palaeo-striatum, from which it is delimited only by a shallow ventricular fissure¹) (fig. 7). It is separated from the archistriatum (in *Varanus*, not in *Lacerta*) by a deep fissure²). It develops partly from the basal wall, partly from the mantle with which it is continuous frontally (fig. 8) and from which cells connected

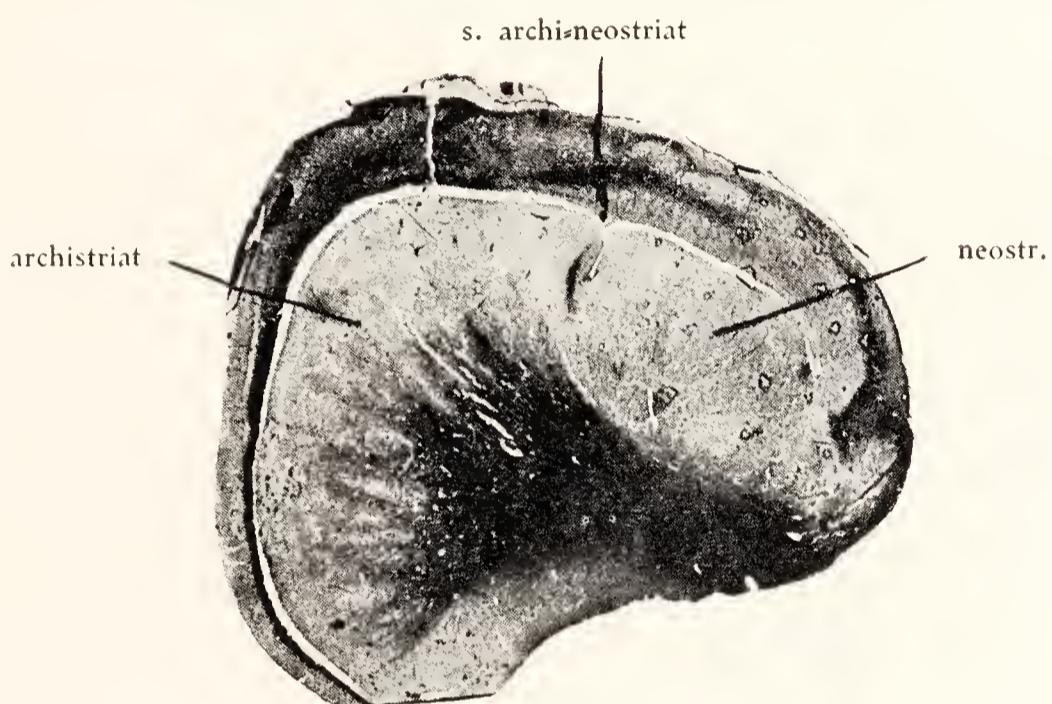


Fig. 6.

Sagittal section of the forebrain of *Varanus salvator*. The tr. cortico-archistriaticus is seen running from the ventral olfactory lobe into the archistriatum.

with the primordium neopallii, may enter it, forming its dorsal layer. Thus the neostriatum, like the archistriatum, is partly a ventricular outgrowth of the pallium (a hypopallial structure, as *Elliot Smith* would call it).

The connections and functions of the neo-striatum are very different from those of the archistriatum, the latter receiving secondary olfactory fibres (fig 6) and the former (fig. 8) receiving ascending fibres from the dorsal thalamus.

¹) Fissura palaeoneostriatica (fig. 8).

²) Fissura archineostriatica (fig. 6, 7 and 8).

As in amphibia the palaeostriatum, which lies centrally, remains chiefly an *efferent centre* of hypothalamic and basal midbrain connections. It also receives some ascending fibres from these regions, but these are few.

As in amphibia, its cells are more or less contiguous with the cells of its ventral thalamic peduncle,¹⁾ or primitive substantia nigra.

The *dorsal thalamus* (see fig. 8) from which fibres arise proceeding to the neostriatum, has become much larger in reptiles through the development of the anterior, medial and small-

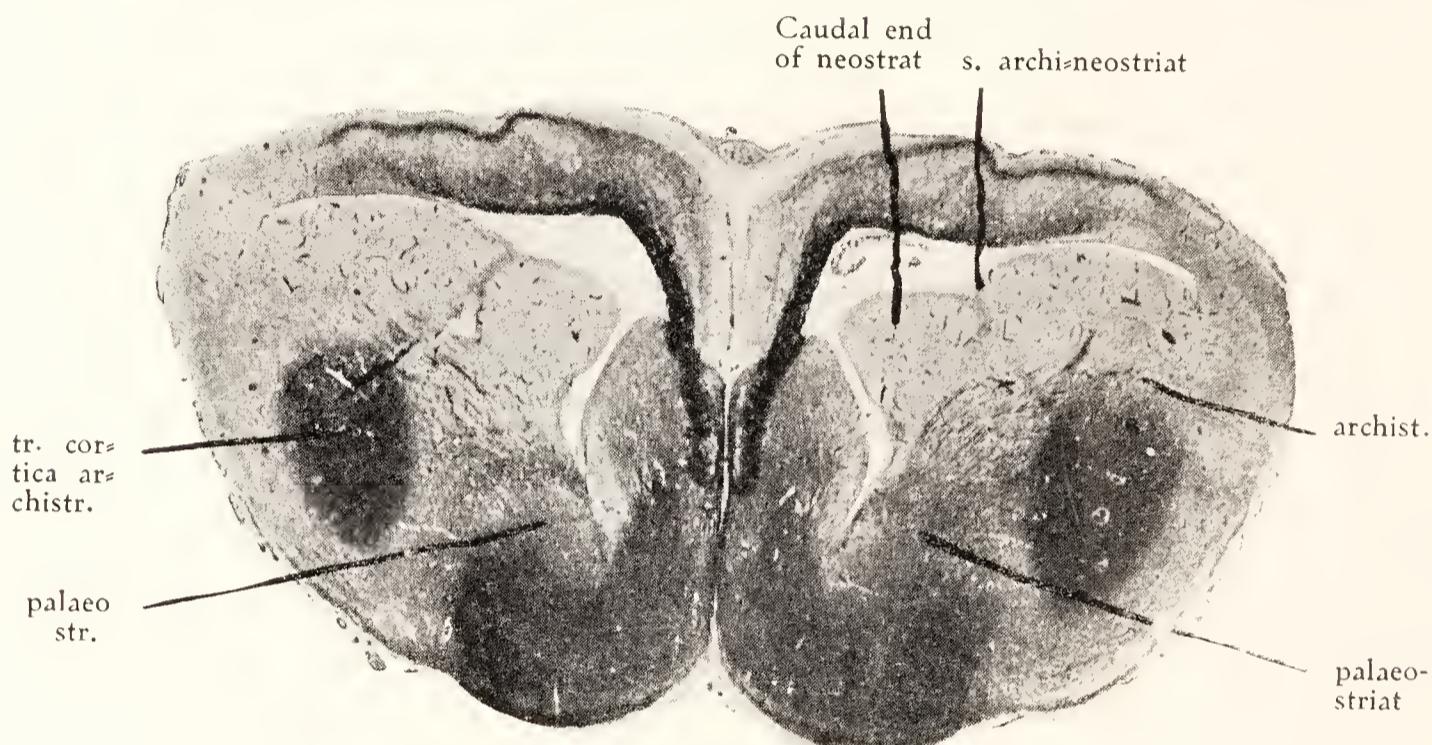


Fig. 7.

Transverse section of the forebrain of *Varanus salvator*. Archistriatum and caudal end of the neostriatum with the palaeostriatum underneath it.

ler ventral nucleus, which together form the *neothalamus*. From these *neothalamic nuclei*, especially from the anterior and medial nuclei, numerous fibres run to the neostriatum.

The character of the impulses thus received, is not exactly known. Probably they are a correlation of impulses from the trigeminus and from the mammillary tweenbrain region, since we know that the medial nucleus (in mammals) is connected with secondary trigeminus fibres, whe-

¹⁾ The palaeo-striatum, however, does not arise from a migration of such cells, as Spatz thought. Paul, who examined its ontogenetic development in Reptiles confirmed my statement that it arises from the forebrain itself.

reas the anterior thalamic nucleus is connected with the hypothalamus, especially the mammillary area. In addition viscerai impulses may occur in it.

We thus see that while the archistriatum is chiefly an olfactory correlation-nucleus, the neostriatum, being connected with the neothalamus, introduces a new function of the forebrain, not present in the frog.

In birds the striatal complex obtains a very large size, which

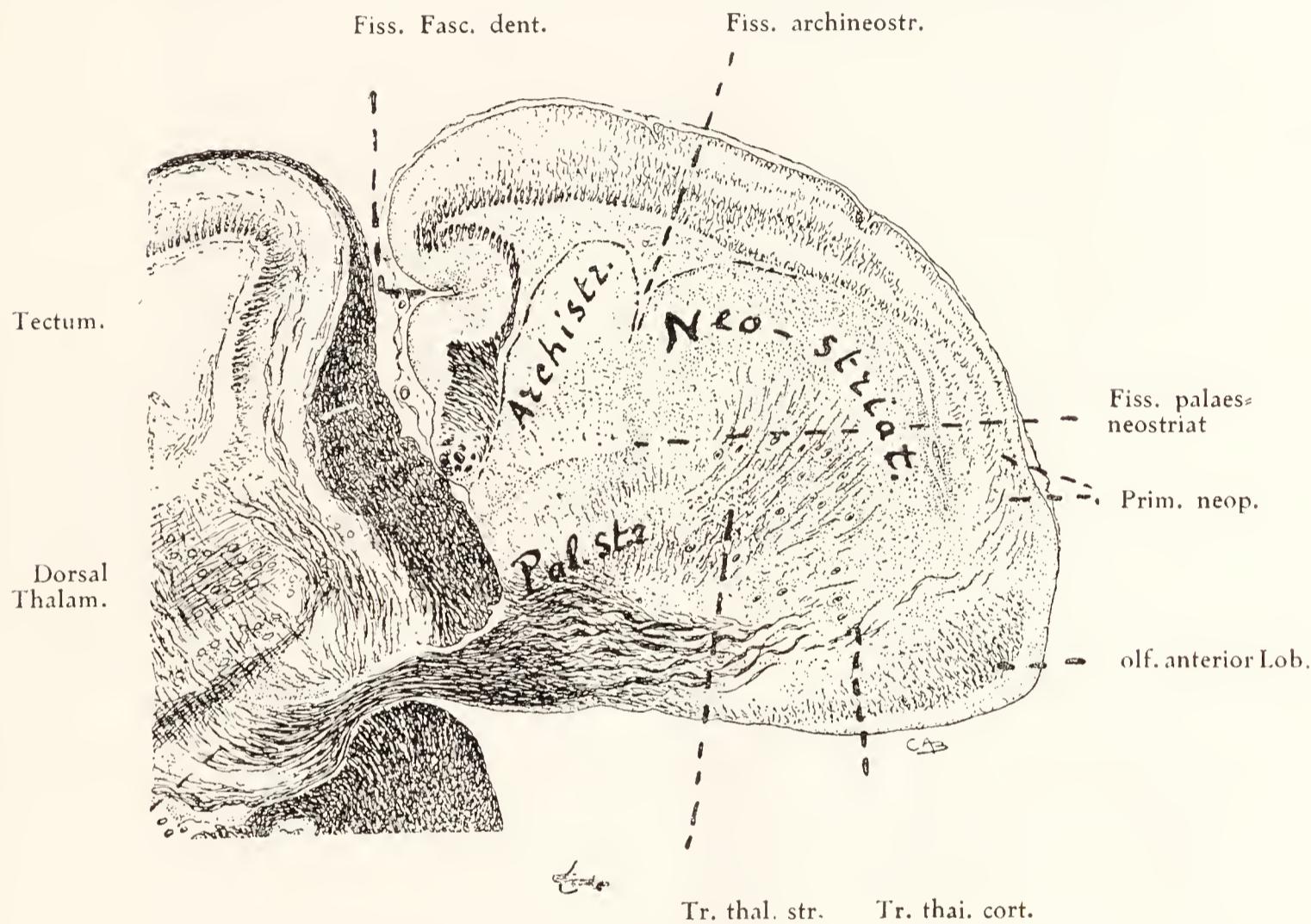


Fig. 8.

Sagittal section through the forebrain of *Varanus*, medially to fig. 3.

is the more striking as the mantle in itself is so poorly developed here. — The same constituents as observed in reptiles are found in birds (fig. 9). The *palaeo-striatum*, developing also here about the level of the foramen Monroi near the praoptic recess, obtains a much larger size. It was described by *Edinger* and *Wallenberg* as the *meso-striatum*. In its centre, the *primitive palaeostriatum* is found as a collection of large efferent neurones (*basal nucleus*) to which, however, a great many

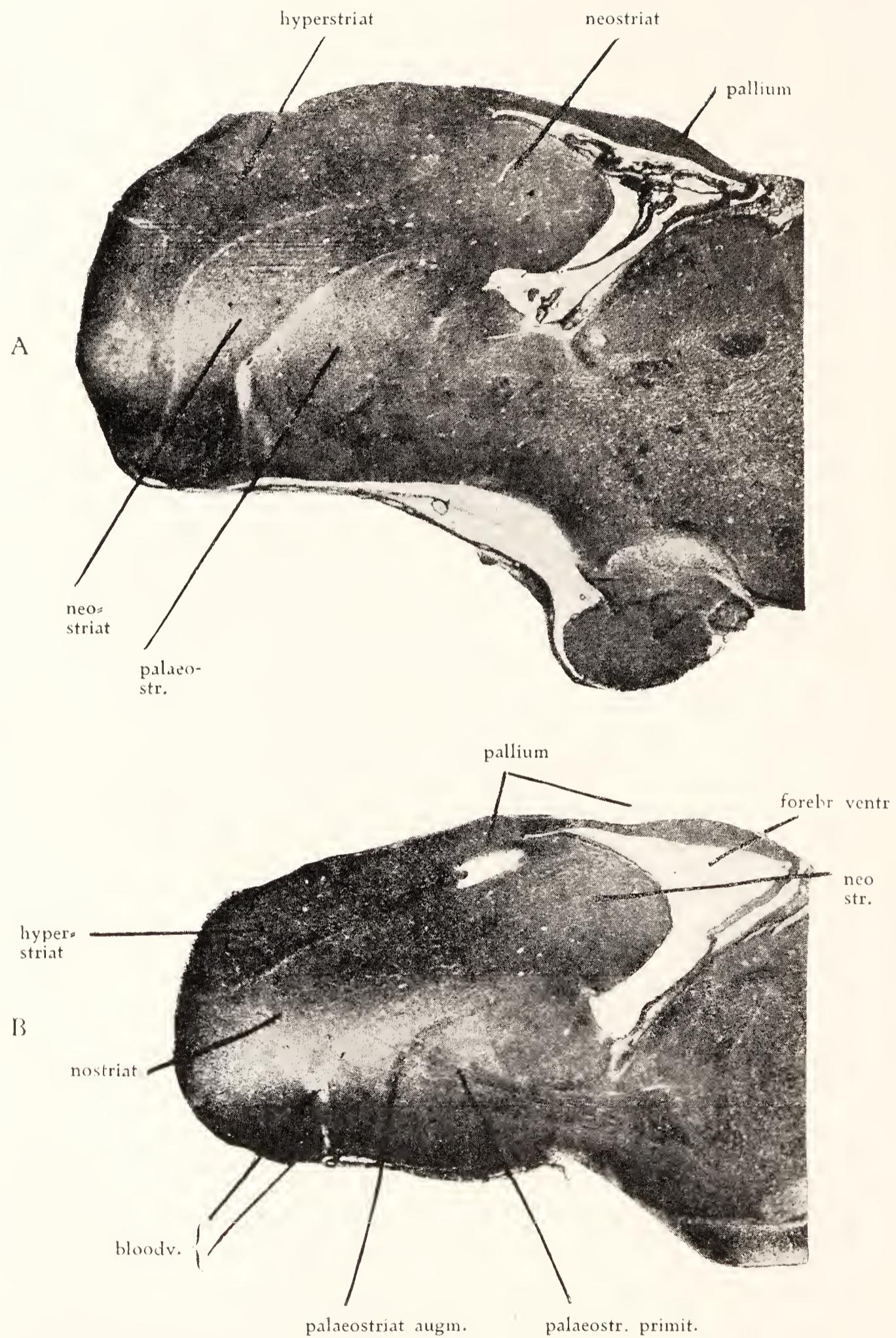


Fig. 9 A and 9 B.

Sagittal section through the forebrain of a chickembryo of the eleventh day of incubation. Fig B is medial to figure A.

cells are added (*palaeo-striatum augmentatum*) indicating a secondary increase of this part, that has cerebellar connections.

I also could state the homology the meso-striatum of birds to the palaeostriatum (*globus pallidus*) of mammals by the sulfur ammonium reaction of *Spatz*, which stains this part blue leaving the neostriatum unstained.

Lateral to and behind the palaeostriatum the *archistriatum* or *amygdala* occurs (hardly cut in the sections of fig. 9). This nucleus is very large in these animals, which seems strange since birds (with the exception of the Kiwi; *Hunter*) are microsmatic.

The size of this nucleus is a strong argument in favor of the conception that the archistriatum is not *only* concerned with olfaction. This is confirmed by the fact that in the region where the cortico-archistriatic tract in these animals arises, the olfactory cortex, is correlated with a strong secondary tract (tr. quinto-frontalis)¹⁾ arising (*Wallenberg*) in the sensory *trigeminus nucleus* of the oblongata from which also fibres proceed to the cerebellum (*Biondi, Craigie*).

This points towards an intimate correlation between olfaction and cutaneous and proprioceptive sense of the head and mouth (oral sense association, *Kappers*), which is easily explained by the frequent correlation between olfaction and movements of the head in search of food (see my first lecture).

As in Reptiles, the archistriata of birds are commissurally connected, and send an efferent tract chiefly to the ventral thalamus and mesencephalon (the tr. occipito- or epistriato-mesencephalicus of *Wallenberg* and *Hermann*).

The *neo-striatum* is much larger than in reptiles, though it develops in the same way, arising partly from the base of the brain, partly from the mantle (see fig. 9 B). Its large size seems to be due to the greater development of the neothalamic nuclei, of which the nucleus rotundus (= nucl. medialis *b* of the crocodile) and nucleus anterior dorsalis, are the most important.

The function of these nuclei, the topography and connections of which in birds were studied by *Edinger* and *Wallenberg*, *Schroeder*, *Craigie*, *Ingvar*, *Crosby* and myself is not easily

¹⁾ Partly crossing, mostly uncrossed.

understood. It is probable, that they are related to correlations in space based on sensory proprioceptive, static and optic¹⁾ impressions, all of which are connected with regulation of movements. It would require too much space to enter into the details of the very intricate network of mutual interrelations between the thalamus and neo-striatum in these animals.

Efferent impulses from the neostriatum run to the midbrain (*Wallenberg*), where they are coordinated with optic and static impulses. These coordinations are probably transmitted by new neurones to the oblongata and the spinal cord.

While the mantle already takes part in the outgrowth of the neostriatum, its role in the development of hypopallial intraventricular masses is still more striking in the avian *hyperstriatum* (*hyperstriatum superior* of *Edinger* c. s.), which might be called *hypopallium kat'exogen*, because it is nothing but an inward growth of the mantle (see specially fig. 9 A). While in early embryonic stages the mantle is still separated from the underlying striatal complex by the ventricle, in adult birds this pallial outgrowth nearly entirely obliterates the ventricle.

The *hyperstriatum* originates from the fronto-dorsal and lateral pallium, growing inwards through the *neurobiotactic influence* (*Elliot Smith, Dart*) of ascending tracts from the thalamus and shorter neuronic connections with the neostriatum, with which it entirely coalesces¹⁾ in the adult.

It seems to replace a surface extension of the (neo) pallium in a way analogous to that in which the primary epistriatum in Teleosts replaces a surface extension of the (palaeo) pallium. Like the epistriatum in Teleosts this peculiar growth may find its origin in influences preventing the mantle from growing out in a normal way (by surface extension), the brain of birds being very narrowly enclosed in the small skull.

In my opinion the *hyperstriatum* in birds has no analogue in mammals. The claustrum of the latter, which has a similar position, is not homologous to it. It may, however, be that it is functionally related to those parts of the mammalian

¹⁾ The nucleus rotundus of birds receives a strong fiber tract from the tectum opticum arising near the ganglion isthmi which ganglion has gravi- and aphototatic functions.

cortex which (according to *Minkowsky, Marinesco, Lhermitte, Coenen* a. o.) are connected with the neostriatum.

The functions of the different parts of the forebrain in birds have been examined experimentally by *Kalisher* in the parrot, and by *Rogers* in the chicken. The former practically stimulated the cortex only, and found that this had a localized influence upon the motility of the animal. *Rogers*, who extirpated parts of the striatum, did not find localized functions in it, but he saw that the more he removed of it the instinctive actions of the animals gradually deteriorated.

These actions were courting and feeding movements, fighting etc. This is interesting, in so far as we know that also in human beings with striatal degenerations the actions of *daily life* are more impaired than »higher« movements. I remember a patient with striatal lesions, who could do all sorts of higher movements¹), apparently cortical, but whose habitual daily life actions were greatly impaired.

This disturbance in the motor functions often has a more or less spastic character, (as also observed in *Parkinson's* disease), and may be due to a disturbance of the tonic innervation. Whether this tonic innervation is of a sympathetic character by the accessory sympathetic muscle fibres of *Boeke (de Boer)* we do not know. It is, however, not impossible since there are also other sympathetic changes after striatal lesions, as e. g. changes of the bladder function, bloodpressure and temperature.

After this short survey of the progressive evolution of the striatum in Amphibia, Reptiles and Birds, we must now consider these parts of the brain in Mammals and man where the *corpus striatum* after *Kinnier Wilson's* discoveries on lenticular degeneration and recent observations on chronic epidemic encephalitis (*Wimmer*²) a. o.) has attracted so much attention.

The *corpus striatum* in Mammals and in man, though developing according to the same principle as in Reptiles, has acquired a very different form. I shall first point out the same principle.

¹⁾ As e. g. writing.

²⁾ Chronic epidemic encephalitis, London, 1924. See also these Acta. Vol. I, 1926, p. 173.

Ontogenetic researches on the corpus striatum of rabbits have convinced me that here also (apart from the archistriatum or amygdala which is connected with the piriform lobe and correlates olfactory impulses)¹⁾ a *palaeo-striatum* and a *neostriatum* may be distinguished, the former arising medially just in front of the praoptic recess, about the level of the foramen of Monro, the latter in front of this, partly from the base of the brain and partly from a fronto-lateral ingrowth of the mantle (crus epirhinicum of *His*, fig. 10: 2).



Fig. 10.

Sagittal section of the forebrain of a 4 cm embryo of *Lepus canis*. At 2 the neostriatum is continuous with the neopallium (above the olfactory ventricle: crus epirrhinicum of *His*).

The palaeo- and neostriatum are originally (see fig. 11), separated by a very conspicuous furrow, the fiss, *palaeo-neostriatica*, but the relation between these two parts soon changes. The neo-striatum, increasing very much in size and growing medially over the palaeostriatum, soon covers this entirely, so that nothing, or only a vestige of the separating furrow, is left on the medial ventricular side of the striatal complex (fig. 12).

¹⁾ I shall not discuss the relations of the amygdala in mammals. For this I refer to *Craigie's* book: The Central nervous System, based upon that of the albino rat. University of Toronto press, 1925, and *Gurdjan*, Journ. of Comp. Neur. 1927.

This considerable increase of neostriatum in comparison to the underlying palaeo-striatum in mammals is an example of the greater increase in higher organized brains (compare the following lecture) of receptive correlative functions in comparison to effector functions, the neostriatum being chiefly a receptory, the palaeo-striatum a effector centre.

In the adult mammal the neostriatum is represented by the *caudate nucleus* and by the *putamen*, the palaeostriatum by the *globus pallidus*, which in Mammals also is continuous with the peduncular cells of the ventral thalamus and midbrain, the cor-

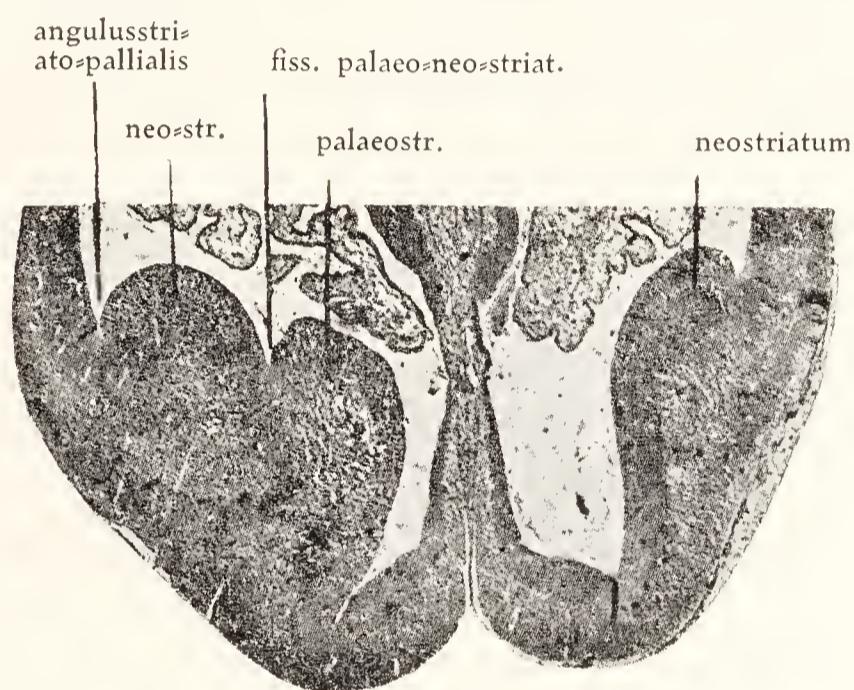


Fig. 11.

Transverse section through the forebrain of a human foetus of 27 mm. The section is slightly oblique. At the left, both the palaeostriatum (medially) and neostriatum (laterally) are seen, separated by the fiss. palaeoneostriatica. In the right half, which is cut more frontally, the palaeostriatum has disappeared.

pus subthalamicum of Luys, and the substantia nigra (being the further development of the peduncular nuclei of birds and Reptiles).

In two¹⁾ respects the striatal complex of mammals differs from that in Reptiles: firstly, by the fact that the neostriatum has

¹⁾ The division made in the neostriatum by the internal capsule in mammals has no intrinsic value. Moreover the location and extension of this capsule varies in different mammals (*E. de Vries*).

considerably increased, and secondly, by its shape. This is a curved one running from the anterior portion of the lateral ventricle along the thalamus to the inferior horn where it joins the amygdala, which remains attached to the backpole of the piriform lobe.²⁾

The elongation of the neostriatum is due to the fact that the whole forebrain develops in a caudal direction, extending back-

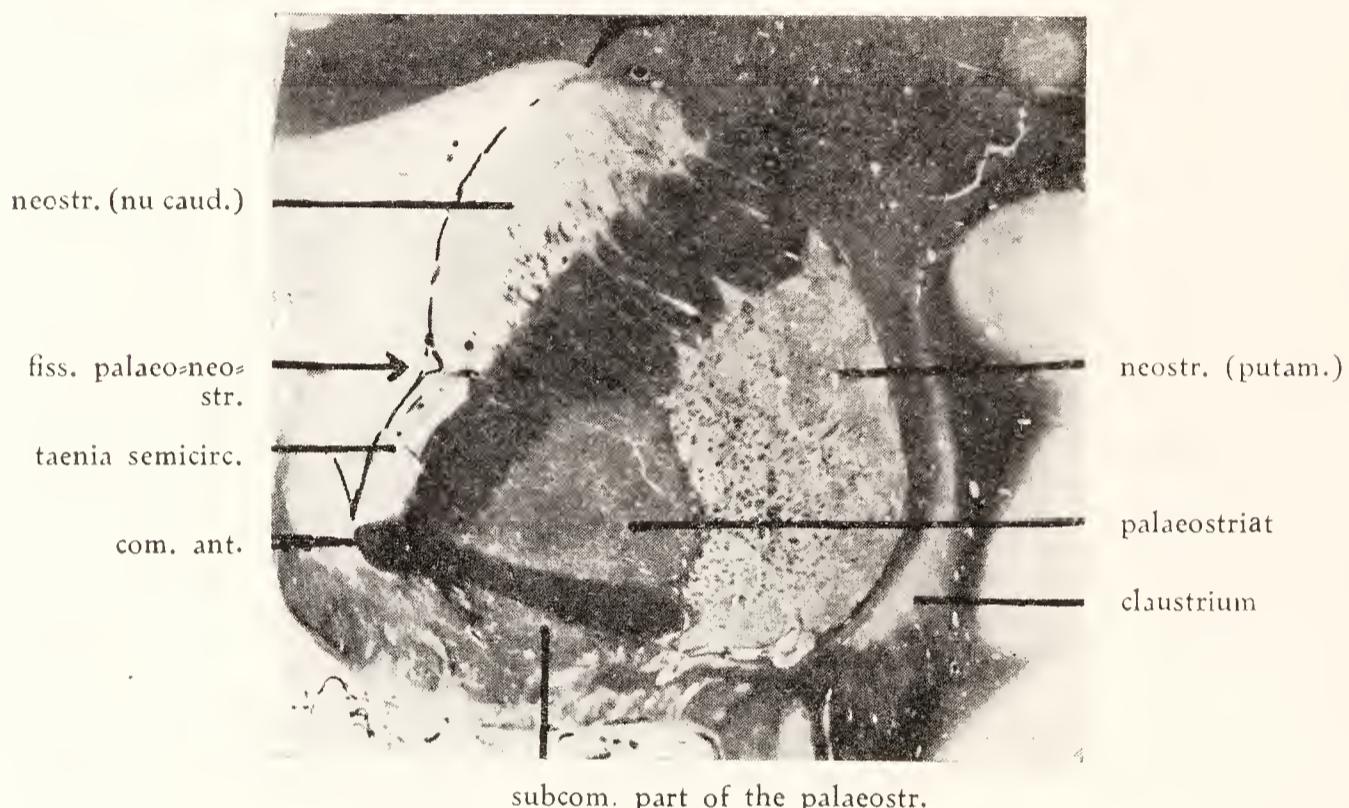


Fig. 12.

Palaeostriatum (globus pallidus) and neostriatum in an adult man. Faintly stained fibers of the taenia semicircularis cover the ventricular side of the palaeostriatum, underneath the fissura-palaeoneostriatica.

wards and downwards.

Although the neostriatum increases in size, much more than the palaeostriatum, its increase does not by any means keep pace with the increase of the neopallium with which it has some, but only few, connections (specially with the anterior and central lobes) as has now been definitely proved in man, by *Minkowski* (in rabbits by *L. Coenen*).

It cannot even be said that the corpus striatum is comparatively best

²⁾ The position of the amygdala is externally indicated on the piriform lobe by *Retzius*' gyrus lunaris and surrounded by the gyrus ambiens (*Elliot Smith*).

developed in man, its size, compared with the brainstem, may even be larger in some lower mammals (*de Vries*).

These connections, however, also prove that there is not only a developmental but also a functional relationship between the neopallium and the neostriatum, a relationship which has been confirmed by the pathological researches of *L. Bouman* and *Bok*, who showed that pathological changes (such as plaques

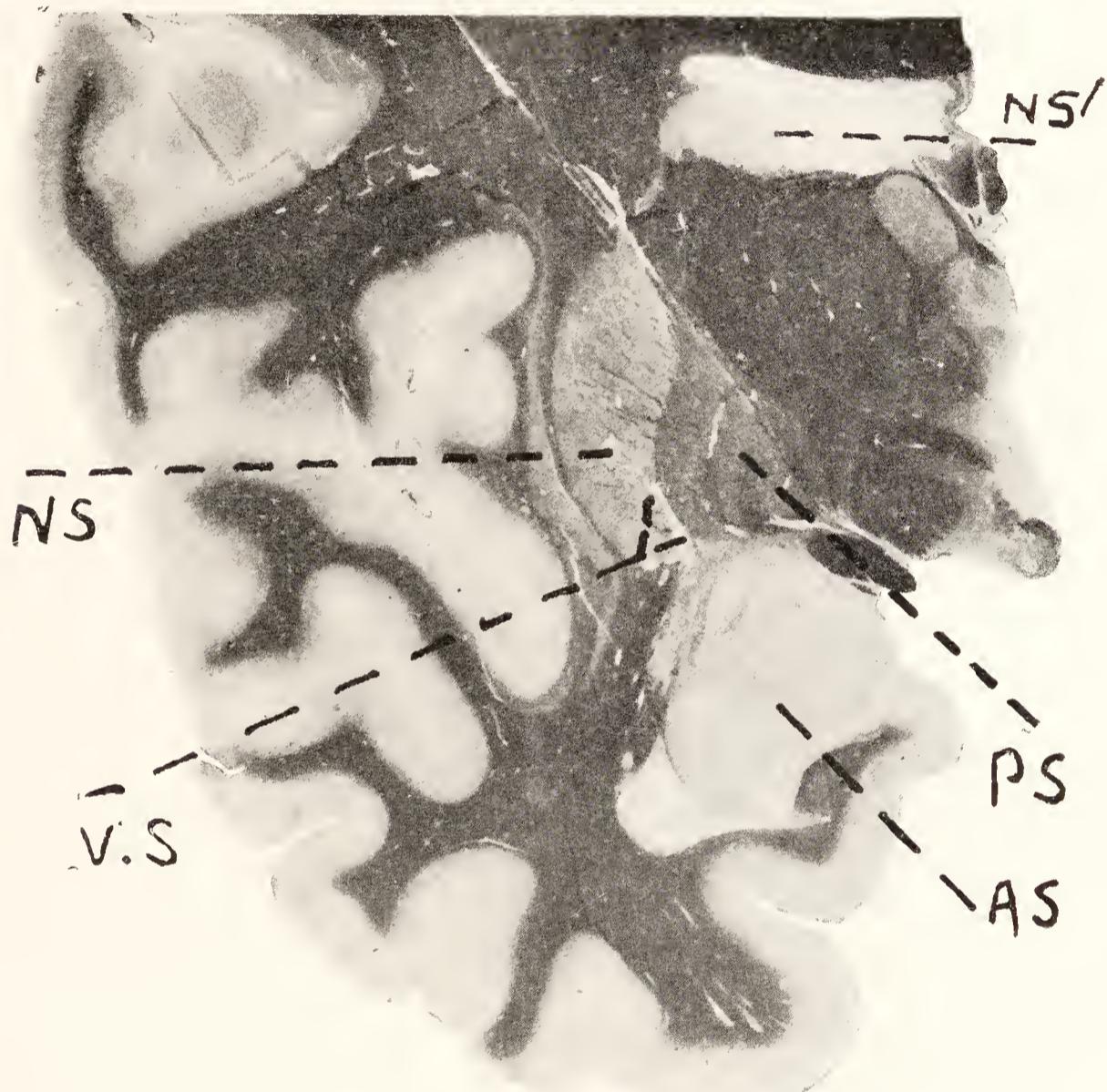


Fig. 13.

Section through the neostriatum (putamen: N s and caudate nucleus: N s') and palaeostriatum (P. s = Globus pallidus). A S = archistriatum or amygdala. A bloodvessel, V. S., separates the palaeo- and neostriatum as it does in birds (fig. 9) and in *Varanus*.

seniles) which affect the cortex, may also affect the neostriatum (not the palaeo-striatum). Moreover *Mills*, already in 1914, pointed out that in spastic disturbances of the face, both the

neostriatum and the adjacent central and frontal neopallium may be affected.

The *functions* of the corpus striatum and the nuclei related to it (substantia nigra, corpus subthalamicum and nucl. ruber) are connected with motility. It is degenerated in spastic diseases such as Parkinson's disease, Wilson's disease, chorea and similar processes, including encephalitis lethargica (*Levaditti, Wimmer*). We do not know, however, exactly on which striatal mechanism these extrapyramidal innervation disturbances depend, but we do know that degenerations of the substantia nigra, the nucleus of *Luys* and those nucl. ruber which are connected with it in a descending (partly also in an ascending) way, may have similar results and often accompany striatal degenerations (*Winkler*).

It is interesting to note that in disturbances occurring in consequence of encephalitis lethargica also the actions, which may be considered actions of daily life, are those that are most impaired. The higher movements which apparently depend more on cortical innervations, may be much less impaired in such cases. *Rogers*'s experiments on birds (see above), which have a large striatum and a small pallium, also speak in favour of an influence on habitual actions.

Apparently the tonic innervation of the muscles is influenced by the striatum. It would be interesting to know whether this has anything to do with the sympathetic or accessory innervation of voluntary muscles discovered by *Boeke*, and experimentally demonstrated by *S. de Boer*.

This is the more interesting since degenerations of the striatum, may be accompanied by other sympathetic disturbances e. g. of the bladder (*van der Scheer and Stuurman, Marburg, Brouwer*), perspiration and of the intestines.

These facts are in accordance with the primary development of the corpus striatum just in front of the ending of the sulcus limitans.

As far as the difference in function between the neo- and palaeostriatum in mammals and man is concerned all the clinical and pathological facts at hand at the present time indicate that we have a relation between those two parts similar to the relation found in Reptiles — the palaeostriatum being more

efferent, the neostriatum more receptory and correlative in function.

As the neostriatum is a new addition to the palaeostriatum and, moreover, increases more than does the latter in birds and mammals (compared with reptiles), their relation reminds us of that in the cortex, in which the receptory-correlative upper layers also increase more phylogenetically than the deeper efferent cortex cells.

I shall discuss this in my last lecture.

THE DEVELOPMENT OF THE CORTEX AND THE FUNCTIONS OF ITS DIFFERENT LAYERS.

The functions of the different layers of the neocortex are a matter of great importance to the neurologist.

The character of the neocortex and the significance of its different layers are, however, most easily understood when compared with the older forms of cortex, the primary olfactory cortex, which I called *palaeocortex*, and the secondary olfactory cortex or *archicortex*.

In the frog, only the two latter regions may be distinguished: the dorso-lateral region being the *palaeocortex* and the dorso-mesial the *archicortex* or primordium hippocampi (fig. 1).

The former receives a large number of olfactory fibres from the *formatio bulbaris*, and, perhaps in addition, some fibres from the dorsal thalamus (*Rubaschkin*). The cortical ending of these fibres is still doubtful and certainly so insignificant in comparison to the former that we are fully justified in calling this cortex a primary olfactory or *palaeo-cortex*.

Its cells (fig. 1) show a very primitive arrangement, being mostly localized near the ventricular ependyma, as is also the case in the mammalian neocortex in an early stage of development (cf. fig. 5).

Most of the dendrites of these cells extend to the lateral surface of the *palaeopallium* (P. Ramon o. a.), to the *tractus olfactorii* that are unmyelinated in frogs (not drawn in fig. 1). The stimuli of these tracts cause their outgrowth in this direction (*neurobiotaxis*, *Kuhlenbeck*).

The *palaeo-cortex* of frogs gradually continues into the

primordium hippocampi, which is not yet differentiated into layers, but whose cells are migrated further away from the periventricular matrix than those of the palaeo-cortex; a consequence of the larger number of fibres running in the superficial zone of the archicortex (tertiary olfactory largely) which fibres, moreover, are myelinated, thus showing a greater functional efficiency.

The cells of the articortex are also larger than those of the palaeocortex, especially the more peripheral ones.

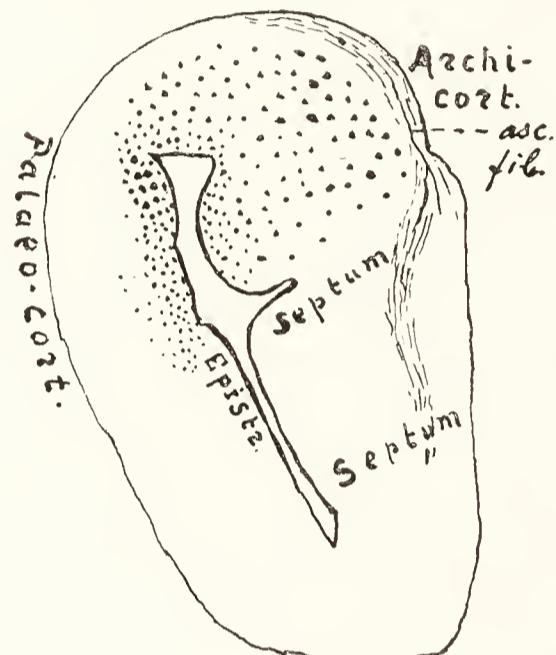


Fig. 1.

Arrangement of cells in the pallium of *Rana esculenta*.

In *Reptiles*, a further differentiation occurs. In *Serpents* and *Lizards* three cortical layers may be observed in the midregion of the hemisphere, more or less joining each other in front and behind. These layers may topographically be called the lateral-, dorsal-, and medio-dorsal layer (fig. 2).

The lateral and dorsal layers consist of large pyramidal cells, but the medio-dorsal layer consists of small granular cells.

In the lateral layer, frontally, the olfactory tract ends. Its frontal part, consequently, is a primary olfactory cortex or *palaeo-cortex*, a primitive homologue of the mammalian prepiriform-cortex in *Brodmann's* nomenclature.

Backward it passes into a sort of piriform cortex and there extends over the archistriatum (the piriform cortex extends into the amygdala in mammals).

Although the frontal part of this cortex is the primitive homologue of the praepiriform cortex and the caudal part corresponds to the piriform cortex of mammals, it everywhere has approximately the same simple structure, in which no distinct layers may be recognized; thus showing a lower plan of organisation than the praepiriform and especially the piriform cortex of mammals (cf. also *Rose, Jacob, Röthig and Kuhlenbeck*).

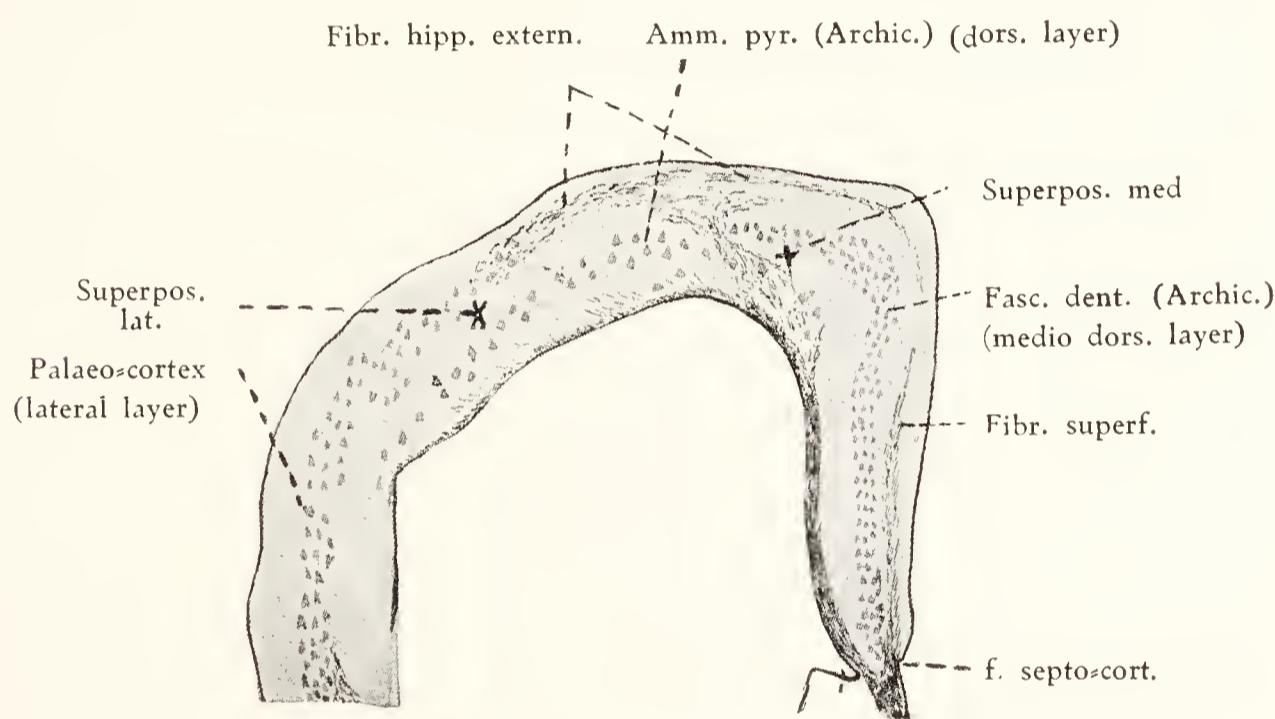


Fig. 2.
Arrangement of the cortical layers in a serpent.

The dorsal and medio-dorsal layer, though different in structure, belong together, establishing the archi- or hippocampal cortex, which, as in mammals, consists of two layers, for the most part adjoining each other, although the medio-dorsal cells lie some what nearer the surface.

The dorsal layer represents the *ammon-pyramids* and the medio-dorsal or granular layer the *fascia dentata* (*Adolf Meyer*).

As in mammals, also in Reptiles, the relation between the *fascia dentata* and the *ammonpyramids* is such, that the latter,

only for a short distance extends below the former as subgranular pyramids.¹⁾

Concerning these two strata of the archicortex, we know that the cells of the granular layer or *fascia dentata*, generally have short neurites (shorter than those of the ammonpyramids, and moreover, mostly arborize in the neighbouring cortex (some extending into the septum).

We also know (*P. Ramon*) that the dendrites of these granular cells all extend to the surface of the mantle, where the ascending tertiary olfactory neurones run. From this it is apparent that this *granular layer or fascia dentata* is a predominant receptive or correlative layer, transmitting the impulses to neighbouring structures only.

Contrary to the latter the cells of the dorsal layer, the ammonpyramids, have large neurites passing into the lining of the ventricle and then leaving the hemisphere to enter either the hemisphere of the opposite side (commissural fibres) or run backward into the hypothalamus, (fornix) and epithalamus (tr. cortico-habenularis). Consequently the *ammonpyramids are cortico-fugal and commissural neurones*¹⁾.

Recapitulating the above said we may say: the archicortex of Reptiles consists of two layers, a receptive (correlative) granular, layer, and a cortifugal and commissural pyramidal layer — which partly extends under the granular layer.

This is the first clear example of a laminar differentiation. It is found again and in the same way in the hippocampus of mammals and the functional division it shows is very instructive as it gives us a key to the understanding of the lamination in the mammalian neocortex.

Before proceeding to the mammalian relations, I shall briefly

- ¹⁾ In Lizards, in addition to these some pyramid cells are lying above the *fascia dentata* (really they are a part of the *fascia dentata* itself, which passes upward and changes its granular character into a pyramidal one).
- ¹⁾ *Elliot Smith* also found a lamination in *Lepidosiren* and an indication of it was found by *Röthig* in *Bufo*. But these laminations are by no means so distinct in their functional significance as those in Reptiles.

discuss the question whether a neocortical primordium is already present in Reptiles.

Doing so we immediately meet with the difficulty of recognizing it, since it is evident, that in lizards we do not find any structure so complicated as in the mammalian neocortex i. e. consisting of several (five- or six)-layers, on top of each other.

Yet there might be a *primordium neopallii* — as *Elliot Smith* called it — in an undifferentiated way.

In order to know if such a primordium neopallii is found in Reptiles we must determine whether or not there are any fibres proceeding from the neothalamus which end in the cortex, since the typical feature of the neocortex is that it does not receive olfactory, but neothalamic projections (sensory, visual etc.).

It is not impossible — it is even likely — that a few of such fibres are found.

As appears in fig. 8 of my 2nd lecture, in Reptiles, a strong tract of fibres runs from the neothalamus to the forebrain, most of them ending in the neostriatum.

Some of these fibres, however, seem to continue their course frontally and laterally beyond the neostriatum and to the mantle. They end (some perhaps begin) in that part of it, where the dorsal edge of the palaeo-cortex stops, or where (in lower Reptiles) it joins the ammonpyramids.

Consequently this spot (*Crosby's* general cortex) lies between the palaeo-cortex and the ammonpyramids of the archicortex.

This proves that, if there is a primordium neopallii, it is represented by cells connected with or arising at the dorsal edge of the palaeo-cortex, in the frontal region of the mantle.

This location is very interesting since we know (cf. fig. 7) that also the mammalian neocortex develops frontally between the palaeocortex (or cortex lobi olfactorii) and archi-cortex (or hippocampus).¹

Whereas, however, even in the lowest mammals (c. f. *Miss Obenchain's* paper on *Caenolestes*) this neocortex is larger and much thicker than either of the other forms of cortex (see fig.

8), in Reptiles it is a mere vestige, only characterized by this fibre-connection and a little thickening of the mantle just in front of the place where the neostriatum is in contact with it.

From the above it appears, that if a vestige of a neocortex occurs in Reptiles, it is only present in the most frontal part of the mantle, lying between the archicortex and palaeo-cortex and connected with the latter.

Proceeding to the cortex of mammals, I shall first discuss the fate of the palaeo- and archicortex in these animals.

The neocortex of mammals, being intercalated between the

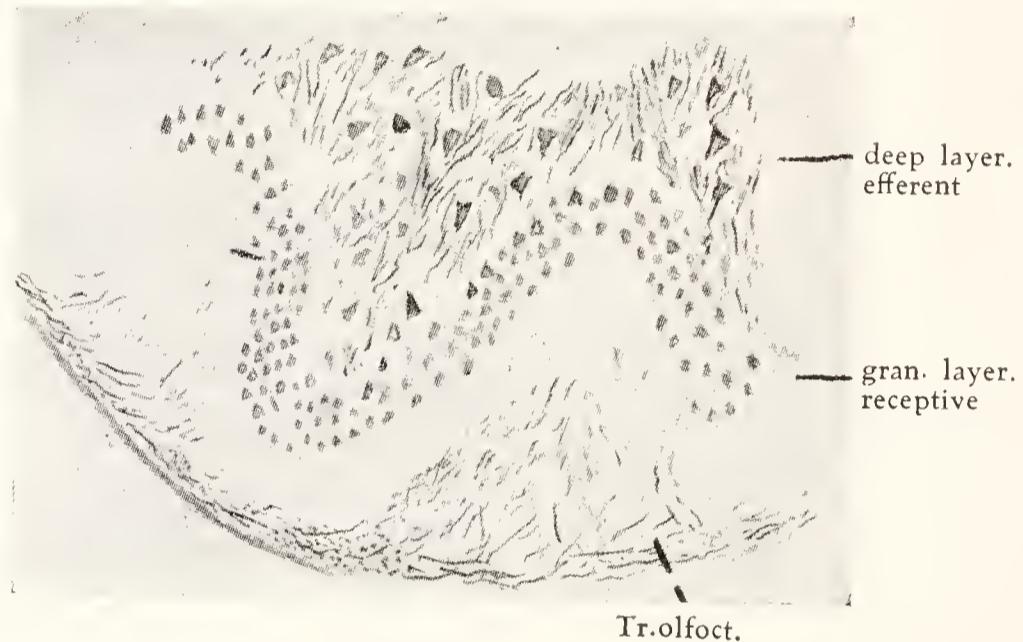


Fig. 3.

Palaeocortex of a Marsupial (*Hypsiprymnus rufescens*).

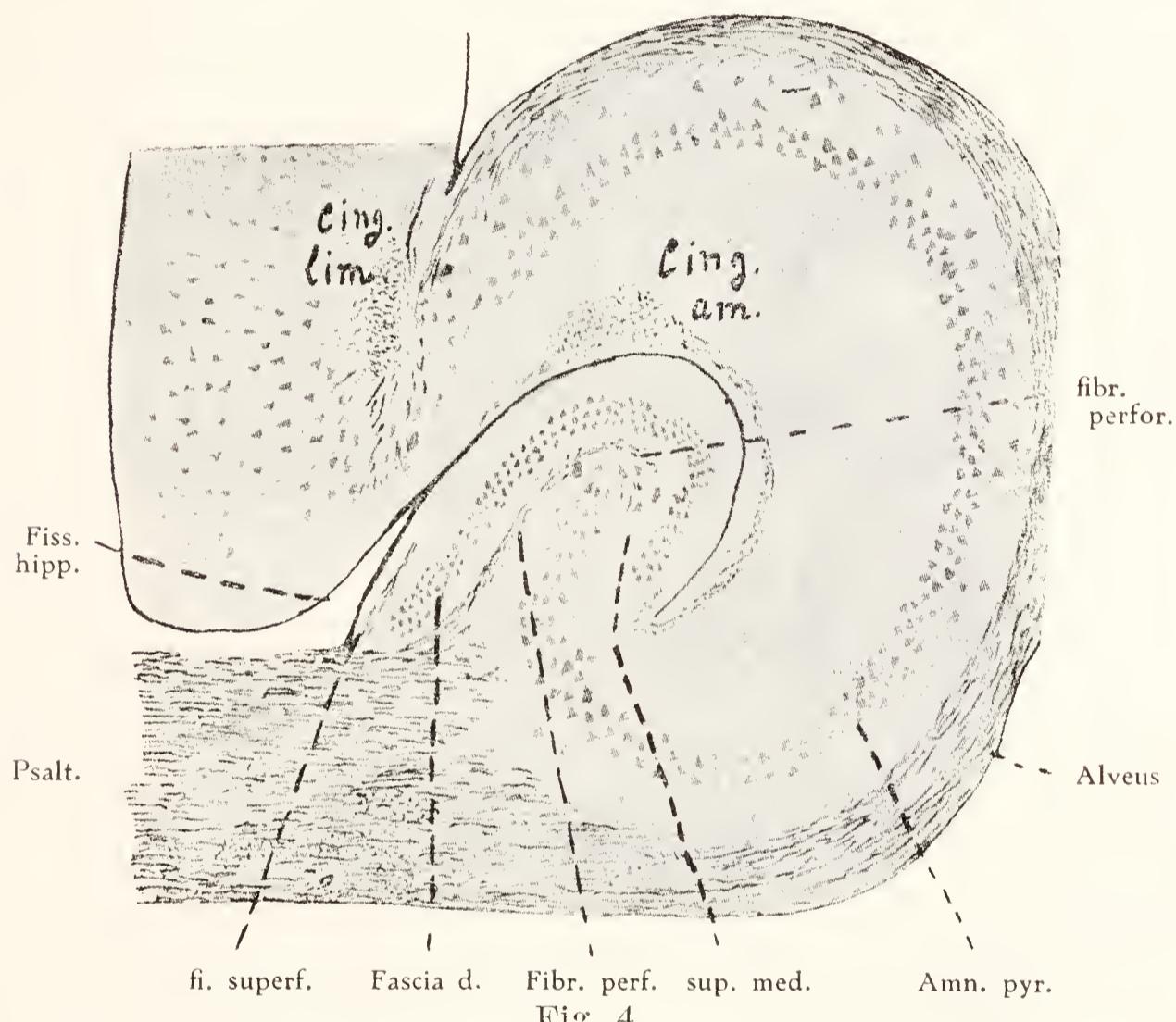
palaeo- and the archi-cortex, its large development in mammals, pushes the *palaeo-cortex* ventrally, causing a limiting fissure between them, the *fissura rhinalis*.

The palaeocortex, or prepiriform cortex of mammals, moreover, shows a higher stage of development, exhibiting two layers (fig. 3) an upper granular and a deep pyramidal layer, the former being mainly receptive-correlative, the latter sending out large efferent tracts to various parts of the fore- and tweenbrain. Apparently we are here dealing with a similar differentiation as in the archicortex, with the difference, however, that in this palaeocortex the different layers lie on top of each other.

On the other hand, the dorsal and medial extension of the

neocortex causes the adjacent pyramidal layer of the archicortex to be lifted up and pushed medially (fig. 4), thus forming the semicircular curve so characteristic of the ammonlayer, the lower point of which remains underneath the hooklike *fascia dentata* (cf. fig. 9).

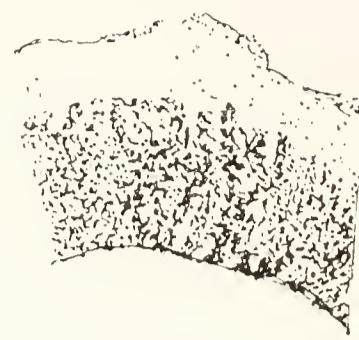
This folding of the ammonpyramidal layer gives rise to the *fissura hippocampi*, which is not a limiting, but an axial furrow lying in the area of the ammonpyramids (not limiting an area



Archicortex and regio cingularis of a Marsupial (*Hypsiprymnus rufescens*).

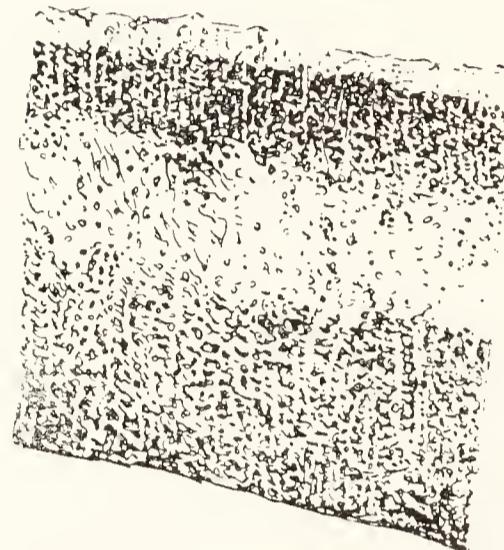
as the fiss. rhinalis does). The cytological difference between the mammalian and reptilian archicortex chiefly consists in a relative increase of ammonpyramids at the expense of the granules of the *fascia dentata* the cells of which apparently are partly embryonic or matrix cells. This corresponds with an increase of fibres of the *psalterium* and *fornix*.

The first development (fig. 5 and 6) of the *neocortex* reminds



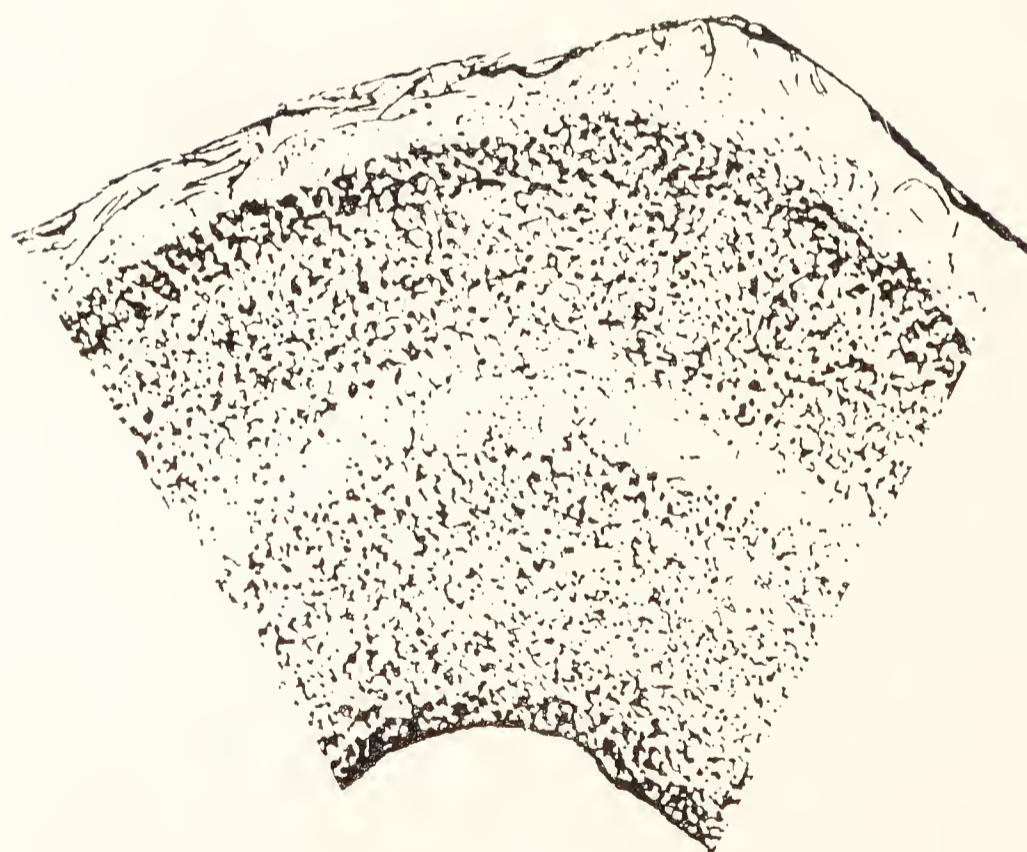
Ventric.
Fig. 5.

Rabbit embryo of 1 cm.



Ventric.
Fig. 6.

Rabbit embryo of 2 1/2 cm.



Ventric.
Fig. 7.

Rabbit embryo of 6 cm.

Different stages of development of the neo-cortex in the rabbit.

us of the arrangement in the palaeo-cortex and archicortex of the frog (cf. the rabbit of 1 c.M. length, fig. 5)¹). All the cells are located in a ventricular matrix, as is the case in the palaeo-cortex of the frog (fig. 1). Only later (fig. 6) some of these matrix cells shift in the direction of the zonal layer²), as it is also observed in the archicortex of *Amphibia*. Still later the neocortex starts to develop into different laminae (fig. 7). In this stage the neocortex is already much thicker than the palaeo- and archicortex. In *Dasypus* (fig. 8) at birth, in man already in a prenatal stage (*Brodmann*) it consists of five cell-layers,³) showing a granular layer (IV) in the middle, and two layers of larger cells in either side of it (above and beneath).

These five cell-layers may, however, be classified in three groups: the *supra-granular cells* (layer II and III of *Brodmann*), the *granular layer* (IV of *Brodmann*), and the *subgranular cells* (V and VI of *Brodmann*).

We shall see that the relation of these three layers to the two layers of the older cortex forms is such, that the granular layer (IV) of the neocortex is homologous to the granular layer of the archicortex (*fascia dentata*), and to the superficial granules of the palaeocortex, while the large subgranular cells (V and VI) of the neocortex are homologous to the ammonpyramids of the archicortex and to the deep pyramids of the palaeocortex.

The supragranular pyramids of the neocortex, however, are a new development, typical of the mammalian neocortex. Though arising from the granular layer they have a more highly developed receptive-associative function than the granule cells.

The laminar homology of the large subgranular cells of the neocortex with the ammonpyramids is seen from the fact that

¹⁾ In the human embryo at the end of the 3rd foetal month the same is observed (*Kuhlenbeck*, *An. Anz.* 1920).

²⁾ This occurs in the human embryo about the 4—5 month (*Kuhlenbeck*).

³⁾ Generally six cortical layers are distinguished, I. zonal layer (which is no cellular layer), II. layer of small pyramidal or stellate cells, III. the supragranular pyramids, IV. the internal granular or granular layer »tout court«, then V. the ganglionic layer and finally VI. the multiform layer. *Campbell's* division is very similar (differing slightly in nomenclature).

the ammon-pyramids continue directly in the subgranular pyramids of the neocortex (fig. 8 and 9), as do also the deep pyramids of the prepitiform cortex. From this also results the homology of the neocortical granular layer (IV) with the granules

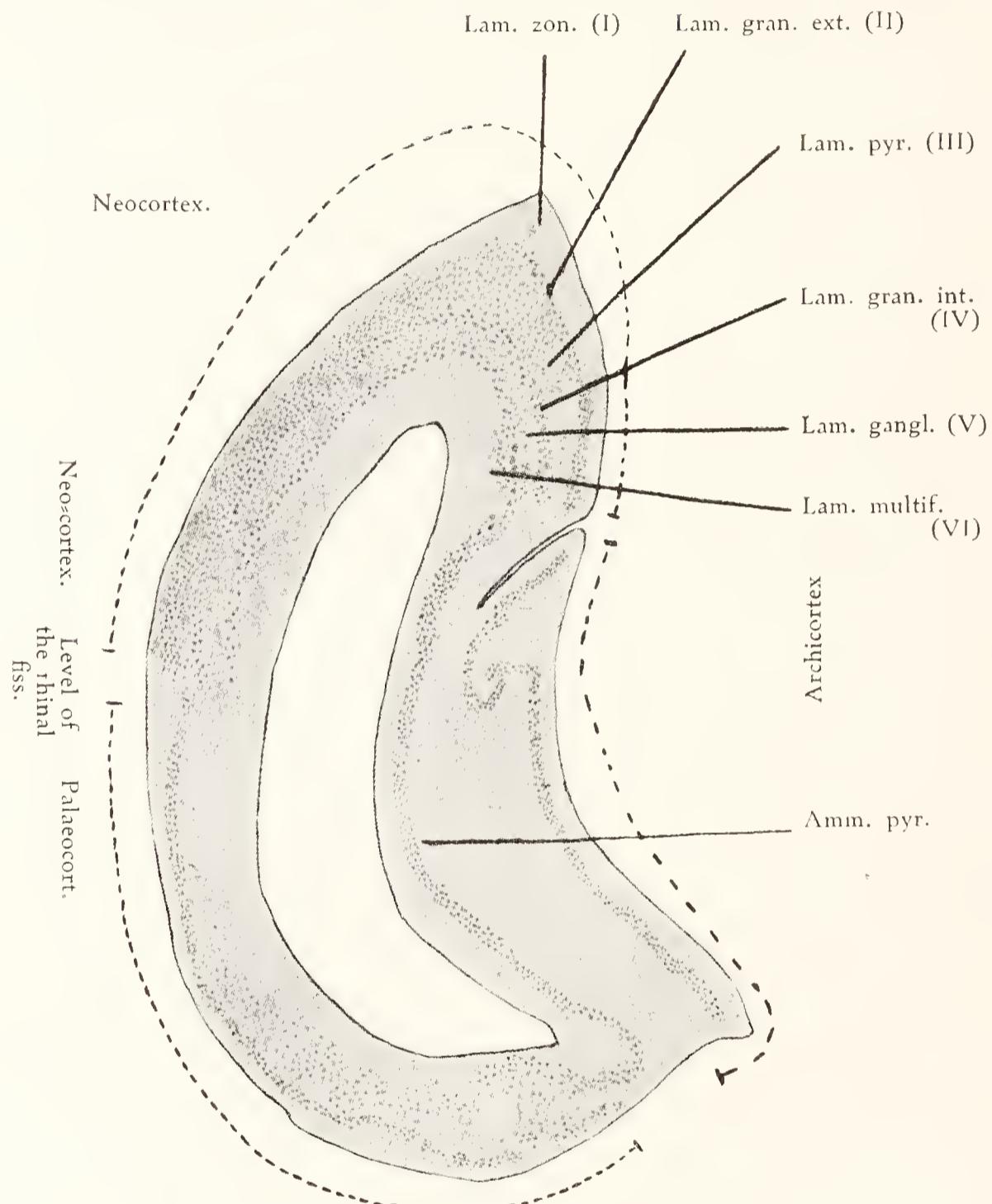
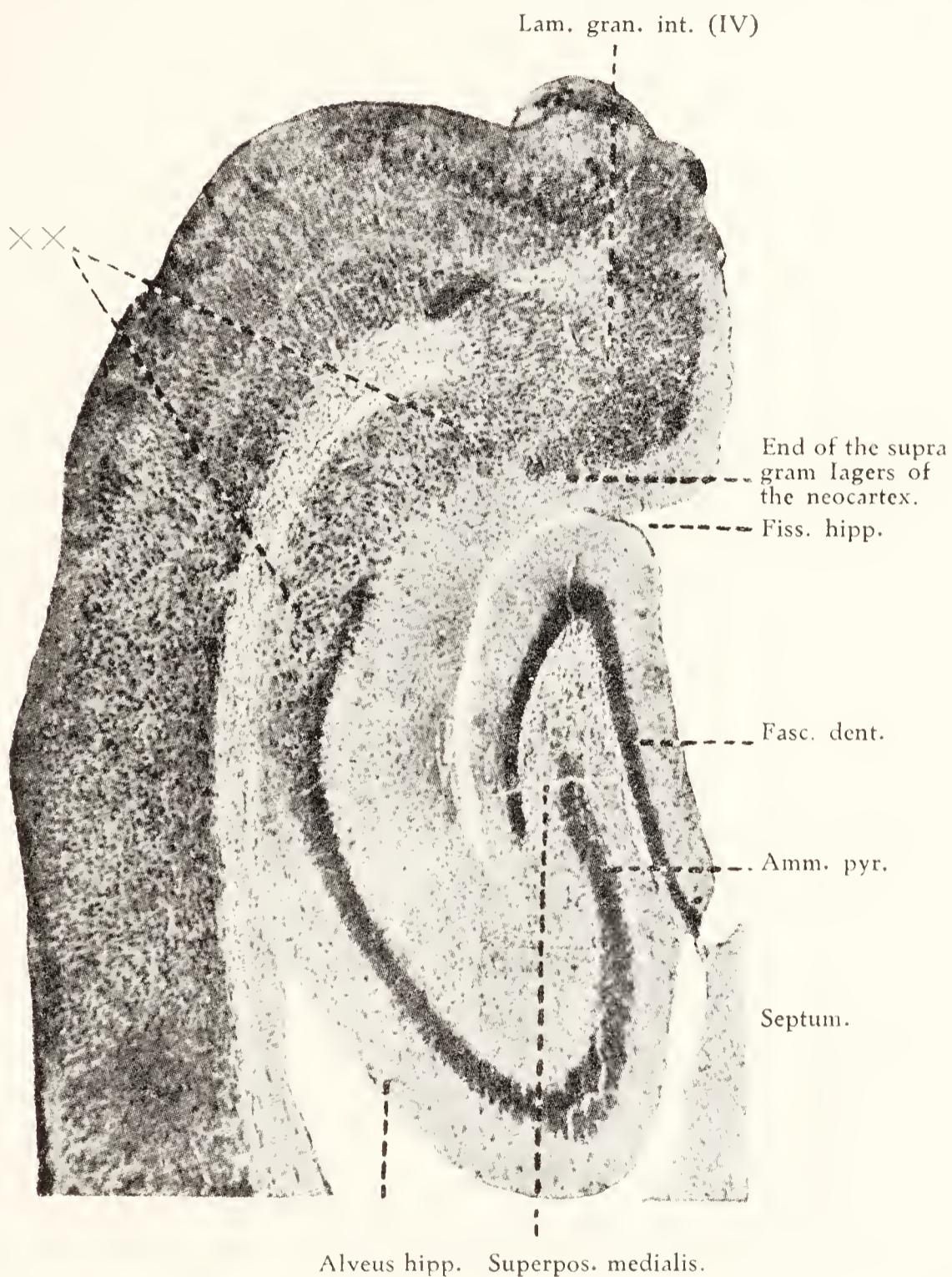


Fig. 8.

Neocortex (exhibiting six layers) between the palaeo- and archicortex in an embryo of *Dasypus novemcinctus*. Note the transition of the ammonpyramids in the subgranular layers (V and VI) of the neocortex.

of the palaeo- and archicortex, as in both cases the deep pyramids lie under these granules (in the archicortex partly under the fascia dentata).

The *function* of the granularis (IV) and of the subgranular pyramids are also the same in the three forms of cortex; the granularis having a correlative—receptive function the subgranular pyramids giving rise to efferent tracts and to commissural fibres. This is seen from the following facts:



Alveus hipp. Superpos. medialis.

Fig. 9.

Transition (of $\times \times$) of the archicortex of an adult rat into the deep layers of the neocortex (cf. fig. 4 and 8).

The granular layer is strongly developed in those regions of the neocortex that have an exquisite sensory function — the postcentral or sensory region, the frontal cortex (which receives

fibres from the nucleus ruber), the auditory and visual cortex. In the area striata (visual cortex) the efferent fibres run in the stria Gennari and Vicq d'Azry, ending chiefly in the granular layer¹). Only few fibres end in deeper layers (*Poljak*).

This does not mean that in the neocortex the granular layer is the only layer which receives afferent impulses. In the sensory (central) and frontal region these impulses also reach the supra-granular pyramids, which, as we shall see, are developed from the granular layer, acquiring larger cellbodies, and developing longer neurites.

On the other hand, the prevailing efferent-commissural and corticofugal character of the subgranular pyramids is shown by the fact that cutting the corpus callosum (*v. Valkenburg, J. dc Vries*) or the centro-fugal tracts (*Holmes and Nissl*) causes a degeneration of subgranular pyramids, while lesions of the supra-granular pyramidal region give no cortico-fugal degenerations, although some of the callosum fibers may also originate here (*Lorente de Nò, vide infra*). — So in the granular and subgranular layer of the neocortex we find a similar localization of functions as in the older cortical areae.

The specific neo-cortical character of the *supra*-granular pyramids, however, is evident, and appears from the fact that in the palaeo- and archicortex on top of the granular layer no layer of pyramidal cells occurs (the few pyramidal cells in which the fascia dentata of Lizards continues dorso-laterally giving off fibers in the zonal layer, may be the only indication of such a process).

Besides the more recent character of the *supra*-granular layer

¹⁾ This granular layer is single in the lower mammals. In primates and man it is doubled. According to *Kleist* the doubling of the granular layer in the striate area of the cortex in primates and man may be explained by a separate course of the crossed and uncrossed visual projection on the cortex, and, according to his opinion, the deeper granular layer (IVb of *Brodmann*) corresponds to the crossed, the higher one (IVa of *Brodmann*) with the uncrossed projection, a conception which — though still wanting experimental confirmation — seems quite possible considering the fact that also in the geniculate body (*Minkowski*) the crossed and uncrossed fibers of the optic tract end in separate layers.

of the neocortex appears from the fact that this layer is the last one to ripen ontogenetically (*Brodmann*).

That, however, the supragranular layer chiefly is an associative extension of the granular layer (IV) is proved by *van't Hoog*, who showed that in animals of the same sub-order but

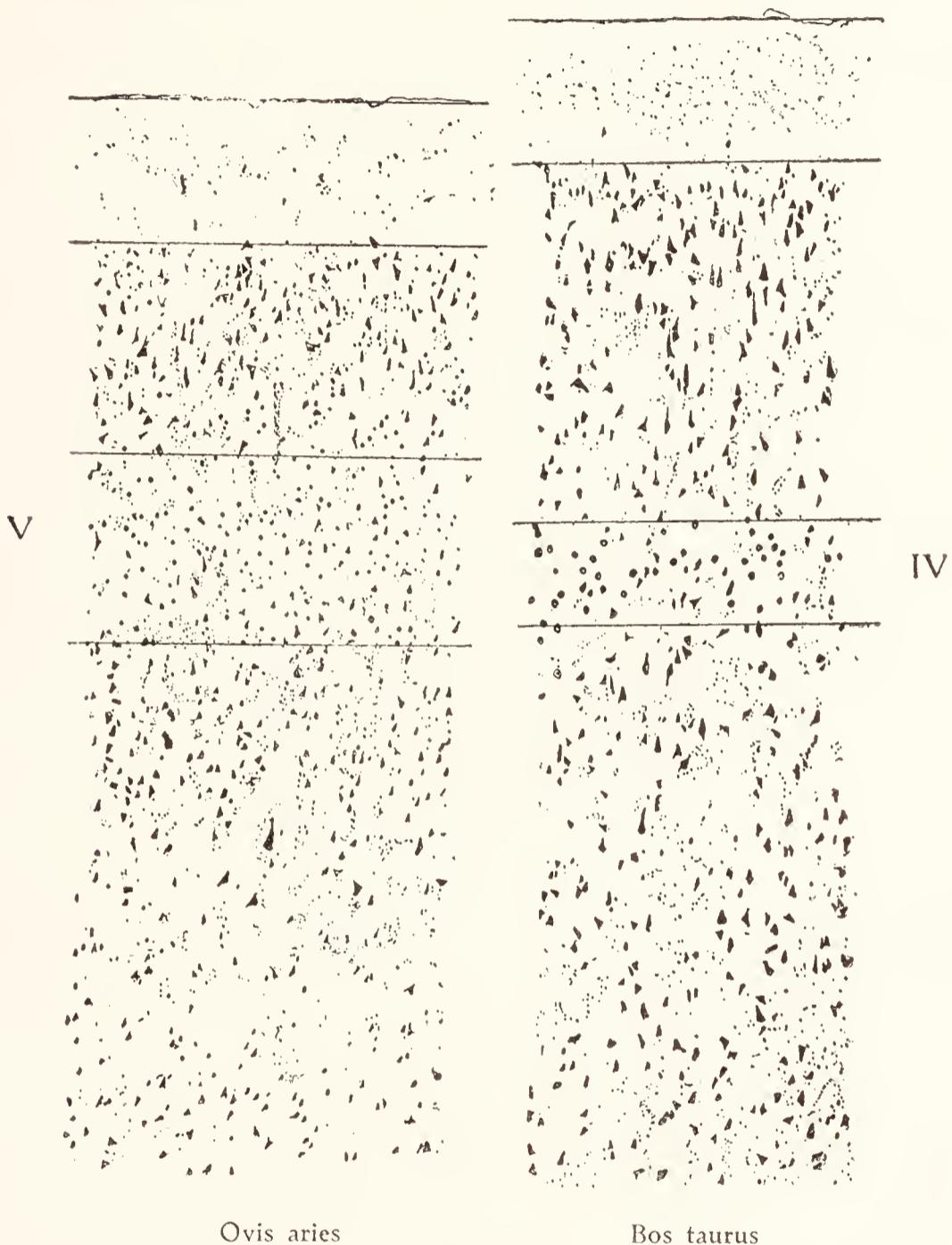


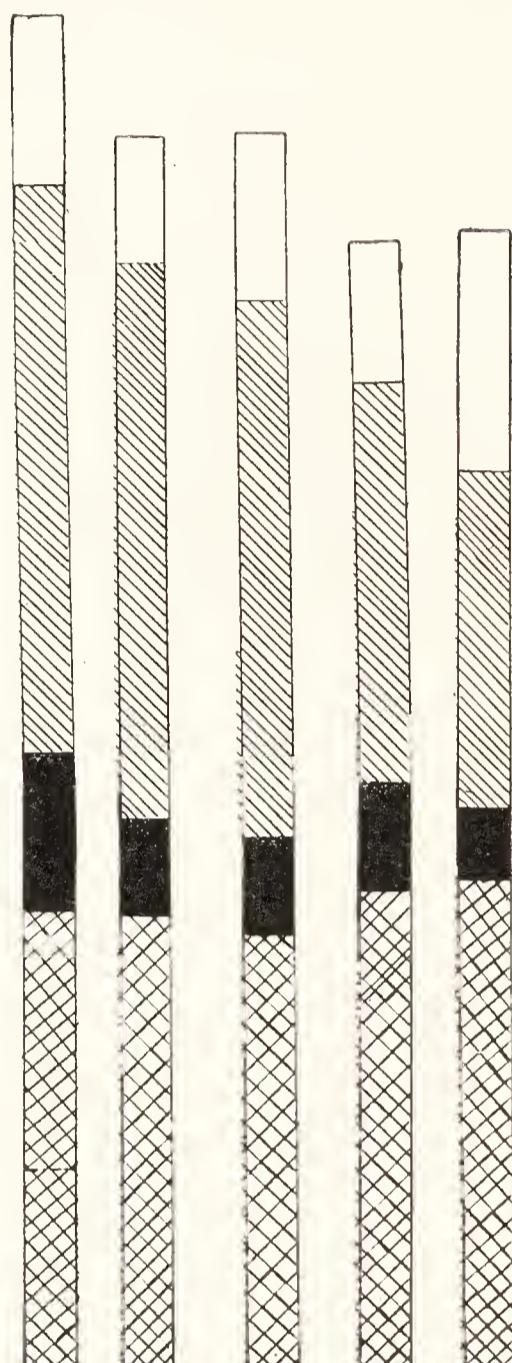
Fig. 10.

The sensory cortex of a small ungulate (sheep) compared to that of a large one (cow) after *van t'Hoog*.

differing in size (as cat and tiger, sheep and cow) in the largest animal the supra-granular cells are increased at the expense of the granular layer, which has become smaller (fig. 10).

This is apparently due to the fact that in large animals sensory functions increase more than motile functions (*Dubois*),

the latter increasing only with the bulk of the muscles, the sensory functions as well with the bulk of the muscles (proprioceptive sensibility), as with the surface of the skin and sense-organs (exteroceptive sensibility).



Homo Troglo- Lemur Felis Rusa
dyes catla leo hipp.

Fig. 11.

Relative development of the supragranular and other layers in an ungulate, carnivore, lemur, shimpanzee and in man. Granular layer black. Supragranular cell layers striped obliquely, subgranular layers crossed.

After van t'Hoog.

Besides in these layers the ending of callosum fibres occurs (*van Valkenburg*).

That the supragranular cells at the same time become larger

than those of the granular layer, may be the result of their axis cylinders (the area covered by it) growing out more in the larger brains, transmitting the received impulses over larger areas of the hemisphere. In addition to receptive they have associative functions, as appears also from the fact that the callosum fibres end here.

Finally the higher, associative character of the supragranular layers appears from the fact, first observed by *Mott* and confirmed by *van't Hoog*, (fig. 11), that in higher mammals this layer is much more developed than in lower ones.

Moreover *Bolton* observed that, in cases of extreme idioey specially, this layer shows a lack of development. A similar conclusion may be drawn from some of the cases described by *Hammarberg*.

The germinal character of the granularis explains that the degeneration of cells in dementia praecox chiefly occurs in that part of the supragranular layer (III) that lies nearest to the granularis, and also in that part of the subgranular cells that lies nearest to the granularis (*Sioli, Alzheimer, O. Vogt, Josephy, Naito, K. H. Bouman*). This may be understood, as *K. H. Bouman* pointed out, by a lack of vitality in the layers that lie nearest the germinal matrix (IV), the more so as also in the granularis itself. *Mott* found a striking lack of basichromatine. Probably this involutive degeneration is an anatomical corollary of the dissociated thoughts and actions (*K. H. Bouman*).

The functional division of the cortex given here, and which I first defended in 1908¹⁾ has recently received several confirmations, (*van Hoog*,²) *Kleist*³⁾ and *Jakob*,⁴⁾ *Kuhlenbeck*⁵⁾ and *Faul*).⁶⁾

¹⁾ *Kappers*. The structure of the palaecortex and archicortex compared with the progressive evolution of the visual neocortex. *Mott's Archives* 1909 and *Phyls Rhinen zephalon, Folia New zohiologica* Bnd. I, 1908.

²⁾ *Van t'Hoog*. Depth localization in the cortex. *Journal of nervous and mental Diseases* 1919.

³⁾ *Kleist*. *Klinische Wochenschr. Jahrg. V, Heft I*, 1926.

⁴⁾ *Jakob*. *Normale und pathologische Anatomie*. Bnd. I der Hirnrinde.

⁵⁾ *Kuhlenbeck*. *Ueber den Ursprung der Grosshirnrinde*. *Anat. Anzeiger*, Bnd. 55, 1922.

⁶⁾ *Faul*. The ontogenetic development of the Claustrum. *Proceed. Kon. Akad. v. Wet. Vol. 26*, 1924.

Resumé.

Summarizing the facts we may say that the primitive arrangement of the cortex as it appears in the palaeo- and archipallium, shows two cell layers, the lamina granularis which has a mainly receptive-correlative function; and the deep-pyramids, having a cortico-fugal and commissural efferent function.

The principle of this lamination is kept up in the neocortex, with this difference, however, that the receptive correlative granular layer, moreover, has given rise to supragranular cells which again are subdivided into two sublaminae as its upper cells still keep a smaller size, while the cells lying nearer the lamina granularis (IV) acquire a pyramidal form.

This differentiation of the supragranular cells does not seem very important. In some parts of the neocortex, in the *regio retrosplenialis* especially, the differentiation of the supragranular laminae even fails.

In this area, according to *Brodmann*, whose observations I can only confirm, the lamina zonalis is still very very wide, the original granular layer (IV) still large, and the lamina supragranularis, between the zonal and granular layer is only poorly developed and shows no subdivision.

As far as concerns the cause of the development of the supragranular layer, *Kuhlenbeck* and later, but independently of him, *Faul*, have given the following neurobiotactic explanation of this process, which is perfectly in accordance with the facts.

As in the palaeo-cortex and in the archicortex the afferent cortical fibres, carrying corticopetal impulses, run in the zonal layer — a fact most fundamentally represented by the primary and secondary olfactory tracts — similarly in the neocortex callosum fibres and part of the ascending thalamic fibres run in the more superficial parts of the cortex, between the surface and the granular layer.

Where thus, the space between the surface and the granular layer originally is an important region for corticopetal impulses it is not strange that these impulses give rise to a much greater outgrowth of matrix cells of the granular layer in a superficial direction, and thus to the formation of supragranular cell-layers, which — in ripening — at the same time acquire a larger size.

Finally I would like to point out that a similar structural arrangement as occurs in the cortex cerebri: the combination of a superficial receptive associative cell-zone with a deeper mainly efferent one and the greater increase of the receptive-associative cells compared to the effectory ones (as also occurs in the striatum)¹⁾ is equally seen in the cerebellum, where the intracerebellar effectory nuclei in higher mammals do not increase as much as the more superficial granules and Purkinje cells do, which receive the impulses and correlate them before leading them via the Purkinje cells to the medial and dentate nuclei.

But even in the organisation of the oblongata a process occurs that points to a relatively greater increase of correlative cells in comparison to effectory cells in higher development.

The fact I refer to is that in lower vertebrates as Sharks, Amphibia and even in Teleosts and Reptiles the motor root nuclei of the oblongata contain only few intercalating (correlative) cells, while in higher animals (mammals chiefly) the motor nuclei appear to consist of root cells to which a great many smaller correlative or reticular neurones are added.

This is especially demonstrated by *Fuse* for the abducens nucleus of mammals in which many cells remain undegenerated after cutting the root. Such a thing is hardly observed in lower vertebrates, where the motor cellgroups are much more simply organised.

This addition of more cells of correlation apparently is a phenomenon of finer adjustment.

CONCLUSIONS.

1) The phylogenetic evolution of the palaeocortex and archicortex shows that the development of cortical gray matter from the periependymal matrix is a neurobiotactic result of the superficial position of the afferent cortical fibre systems, as rightly pointed out by *Kuhlenbeck*.

¹⁾ See my second lecture.

2) The first differentiation, as it is found in the archicortex of Reptiles and the palaeo- and archicortex of Mammals, gives rise to only two different cell-layers; a granular receptive layer near the surface where most afferent impulses run, and a deeper, or subgranular, efferent pyramidal layer.

3) In the neocortex, in addition to these two layers a third layer develops more superficially forming the *supra-granular* cells which develop from the *granularis*. The development of these cells is a consequence of the increase of cortico-petal and associative fibers.

4) If callosal fibers do not only end (*v. Valkenburg*) but partly also originate in supra-granular pyramids (*Lorente de Nò*) this would only more emphasize the associative function of this layer.

5) The correlative character of the supra-granular cells also accords with the fact that in higher animals these cells increase much more than any other layer of the cortex.

6) A similar increase of receptive correlative cells in comparison to effector parts is observed in the striatum, the cerebellum, and in the motor centers of the oblongata.



